

ROTYLENCHULUS SPECIES: IDENTIFICATION, DISTRIBUTION, HOST RANGES, AND CROP PLANT RESISTANCEA. F. Robinson,¹ R. N. Inserra,² E. P. Caswell-Chen,³ N. Vovlas,⁴ and A. Troccoli⁴

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ABSTRACT

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The ten known species of *Rotylenchulus* are sedentary root parasites that occur largely in tropical and subtropical latitudes. They can be distinguished with a simple dichotomous key. Hundreds of studies have examined the biology, economic impact, and management of the type species, *R. reniformis*. Information also is available regarding the geographical distribution, host range, and histopathology induced by *R. borealis*, *R. macrodoratus*, *R. macrosoma*, and *R. parvus*. Relatively little is known regarding *R. anamictus*, *R. brevitubulus*, *R. clavicaudatus*, *R. leptus*, and *R. sacchari*. *Rotylenchulus reniformis* and *R. parvus* both appear to have a cosmopolitan distribution in warm latitudes; *R. borealis*, so far, has been reported primarily from Europe and Africa; *R. macrodoratus* and *R. macrosoma* have been found primarily in the Mediterranean region. There are clear anatomical differences in the trophic site induced by *R. macrodoratus* (uninucleate giant cell) compared to those induced by *R. borealis*, *R. macrosoma*, *R. parvus*, and *R. reniformis* (syncytia). There also are differences in the abilities of these species to parasitize various hosts. *Rotylenchulus reniformis* appears to have the widest host range and has been reported to reproduce on 86% of 364 plant species examined. Many common weeds are good hosts. However, more than 50 crop or ornamental plants support little or no reproduction by most populations of *R. reniformis*. Examples include barley, maize, onion, rice, several crotalaria species, and resistant cultivars of soybean. Varying levels of resistance also have been found in cotton, olive, papaya, potato, sweet potato, tobacco, tomato, and various legumes. Most research on crop rotation and mixed cropping for management of *R. reniformis* has been done on cotton and soybean in the United States, and on legumes in India.

Key words: biology, crop rotation, distribution, host range, quarantine, reniform nematodes, *Rotylenchulus anamictus*, *Rotylenchulus borealis*, *Rotylenchulus brevitubulus*, *Rotylenchulus clavicaudatus*, *Rotylenchulus leptus*, *Rotylenchulus macrodoratus*, *Rotylenchulus macrosoma*, *Rotylenchulus parvus*, *Rotylenchulus reniformis*, *Rotylenchulus sacchari*.

RESUMEN

Robinson, A. F., R. N. Inserra, E. P. Caswell-Chen, N. Vovlas y A. Troccoli. 1997. Las especies de *Rotylenchulus*. Identificación, distribución, rangos de hospederos y resistencia de cultivos. *Nematropica* 27:127-180.

Las diez especies conocidas de *Rotylenchulus* son parásitos sedentarios de raíces y se encuentran principalmente en latitudes tropicales y subtropicales. Se pueden diferenciar con una simple clave dicotómica. La biología, la importancia económica y el control de la especie tipo, *Rotylenchulus reniformis*, han sido el objetivo de centenares de investigaciones. También se dispone de información sobre la distribución geográfica, el rango de hospederos y la histopatología inducida por *R. borealis*, *R. macrodoratus*, *R. macrosoma* y *R. parvus*. Se conoce poco sobre *R. anamictus*, *R. brevitubulus*, *R. clavicaudatus*, *R. leptus* y *R. sacchari*. La especie *R. reniformis* y *R. parvus* presentan una extensa distribución en latitudes cálidas. *Rotylenchulus borealis* se encuentra principalmente en Europa y África, mientras que

R. macrodoratus y *R. macrosoma* se localizan en la región Mediterránea. *Rotylenchulus macrodoratus* induce la formación de una célula gigante mononucleada en la zona estelar de la raíz mientras que *R. borealis*, *R. macrosoma*, *R. parvus* y *R. reniformis* producen un sincitio. Existen diferencias entre las tasas de reproducción de *R. reniformis*, *R. parvus* y *R. borealis* en varios hospederos. *Rotylenchulus reniformis* parece tener un rango de hospederos más amplio que las otras especies de este género y se reproduce en 86% de las 364 especies de plantas examinadas. Muchas malezas comunes son buenos hospederos. Sin embargo, más de 50 plantas agronómicas y ornamentales permiten poca o ninguna reproducción de *R. reniformis*. Ejemplos incluyen arroz, cebada, cebolla, maíz, varias especies de crotalaria y cultivos resistentes de soya. Se encuentran también diferentes niveles de resistencia en el algodón, olivo, papaya, papa, batata, tabaco, tomate y varios cultivos leguminosos. La mayoría de las investigaciones sobre la rotación de cultivos para manejar poblaciones de *R. reniformis* han sido realizadas en algodón y soya en los Estados Unidos y en varios cultivos leguminosas en la India.

Palabras claves: biología, cuarentena, distribución, nemátodos reniformes, rango de hospederos, rotación de cultivos, *Rotylenchulus anamictus*, *Rotylenchulus borealis*, *Rotylenchulus brevitubulus*, *Rotylenchulus clavicaudatus*, *Rotylenchulus leptus*, *Rotylenchulus macrodoratus*, *Rotylenchulus macrosoma*, *Rotylenchulus parvus*, *Rotylenchulus reniformis*, *Rotylenchulus sacchari*.

INTRODUCTION

Reniform nematodes (*Rotylenchulus* spp.) are semi-endoparasites of roots and occur commonly in tropical and subtropical regions. The term "reniform" refers to the kidney-shape of the body of the sedentary mature female. Ten valid species of *Rotylenchulus* are known. *Rotylenchulus reniformis* is the most economically important and has the widest geographical distribution and host range. It was described in 1940 by Linford and Oliveira from specimens collected in Hawaii, U.S.A., and for more than 20 years was the only representative of the genus. In 1961, a second species, *R. parvus* (Williams, 1960), was transferred from the genus *Helicotylenchus* into the genus *Rotylenchulus* by Sher. In 1962, a third species, *R. borealis*, was described from The Netherlands by Loof and Oostenbrink. Five additional species from Africa (*R. anamictus*, *R. clavicaudatus*, *R. leptus*, *R. macrosoma*, and *R. variabilis*) and one from Italy, (*R. macrodoratus*) were described by Dasgupta *et al.* in 1968. *Rotylenchulus variabilis* was later synonymized with *R. borealis* (Germani, 1978a). Subsequently, two more species, *R. sacchari* (Van

den Berg and Spaull, 1981) and *R. brevitubulus* (Van den Berg, 1990), have been described from South Africa.

Taxonomic descriptions for some *Rotylenchulus* species are incomplete; for instance, mature females of *R. anamictus*, *R. brevitubulus*, *R. leptus*, and *R. sacchari* are unknown. Also, type hosts of *R. anamictus*, *R. brevitubulus*, *R. clavicaudatus*, *R. leptus*, and *R. sacchari* were not determined. In the case of *R. clavicaudatus*, only one mature female was found in the rhizosphere of sugarcane (*Saccharum officinarum*), making the identity of the type host plant uncertain. Valid species of the genus *Rotylenchulus*, their type host(s), and the author(s) of each species description are listed in Table 1.

Type localities of known *Rotylenchulus* species (Table 1) reflect the largely tropical and subtropical distributions of these root parasites. Even *R. borealis*, which was originally found in The Netherlands, has been reported in several African countries where it was confused with *R. variabilis*, its junior synonym (Germani, 1978a). Although several reniform nematode species may ultimately prove to be important pests on some crops, *Rotylenchulus reniformis*

Table 1. Species of the genus *Rotylenchulus*.

Species	Type host	Type locality	Author(s)
<i>R. anamichus</i> *	Associated with <i>Acacia</i>	Somalia	Dasgupta <i>et al.</i> , 1968
<i>R. brevitubulus</i> *	Unknown	South Africa	Van den Berg, 1990
<i>R. borealis</i>	Maize (<i>Zea mays</i> L.)	The Netherlands	Loof & Oostenbrink, 1962
<i>R. clavicaudatus</i>	Associated with <i>Strelitzia</i> and sugarcane (<i>Saccharum officinarum</i> L.)	South Africa	Dasgupta <i>et al.</i> , 1968; Van den Berg & Spaull, 1981
<i>R. leptus</i> *	Associated with bamboo (<i>Bambusa vulgaris</i> Schard. ex J. C. Wendl.)	Zimbabwe	Dasgupta <i>et al.</i> , 1968
<i>R. macrodoratus</i>	Grape (<i>Vitis vinifera</i> L.)	Italy	Dasgupta <i>et al.</i> , 1968
<i>R. macrosoma</i>	Olive (<i>Olea europaea</i> L.)	Israel	Dasgupta <i>et al.</i> , 1968; Cohn & Mordechai, 1988
<i>R. parvus</i>	Sugarcane (<i>S. officinarum</i>) and Upland cotton (<i>Gossypium hirsutum</i> L.)	Mauritius and California (USA)	Williams, 1960; Dasgupta <i>et al.</i> , 1968
<i>R. reniformis</i>	Pineapple [<i>Ananas comosus</i> (L.) Merrill]	Hawaii (USA)	Linford & Oliveira, 1940
<i>R. sacharr*</i>	Associated with sugarcane	South Africa	Van den Berg & Spaull, 1981

*Species with undescribed mature females.

mis is the only species proven so far to be economically important and it is by far the most intensely investigated. It has been the subject of numerous studies related to life cycle, host range, host-parasite relations, plant damage, behavior, survival, and management. Biological studies on other species are limited to *R. borealis*, *R. macrodoratus*, *R. macrosoma*, and *R. parvus*.

Life cycle: All *Rotylenchulus* species studied so far have a generally similar life cycle. One-celled eggs are oviposited by mature females. Embryogenesis is completed with the appearance of the first-stage juvenile (J1) which molts within the egg shell, producing the second-stage juvenile (J2) that emerges from the egg. The J2 and following juvenile stages (J3 and J4) are not parasitic and retain the cuticles of the previous stages after molting (Fig. 1). The body of *R. reniformis* is slightly shorter and smaller in volume rather than larger after each molt (Bird, 1983). Eight species of *Rotylenchulus* have both females and males (Dasgupta *et al.*, 1968; Van den Berg, 1990; Van den Berg and Spaull, 1981). In *R. reniformis*, the final molt gives rise to approximately equal numbers of vermiform parasitic females and nonparasitic males. *Rotylenchulus parvus* and some populations of *R. reniformis* reproduce parthenogenetically (Dasgupta and Raski, 1968; Nakasono, 1983). Most or all of the vermiform adults produced by the final molt in these populations are females; males are rare or absent.

In the presence of host roots, vermiform females penetrate the root cortex, establish a permanent feeding site in the stele and become sedentary (Fig. 2A,B). The anterior part of the body remains embedded in the root whereas the posterior portion protrudes from the root surface and swells during maturation of the reproductive system, assuming a kidney-like shape (Figs. 2D,E). In the stele, the infective females induce the formation of

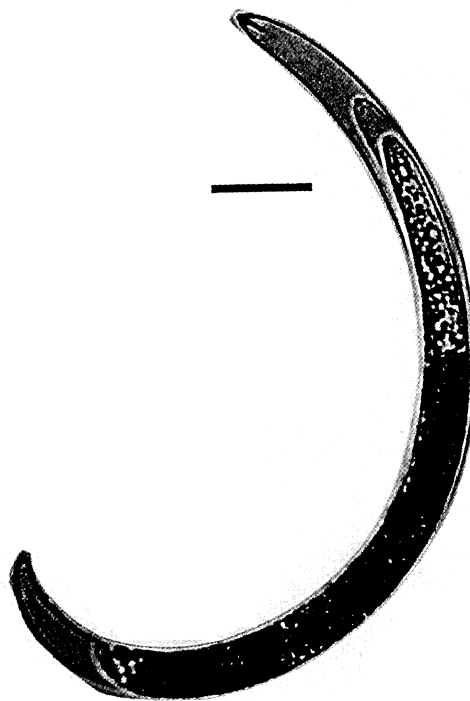


Fig. 1. Fourth-stage juvenile of *Rotylenchulus macrodoratus* enveloped by two cuticles. Scale bar = 34 μ m. (After Inserra and Vovlas, 1980).

specialized trophic sites involving stelar tissues (Fig. 2D,E) (Cohn and Mordechai, 1977; Rebois *et al.*, 1975; Vovlas *et al.*, 1985). Soon after gonad maturation, females deposit eggs into a gelatinous matrix (Fig. 2E). The gelatinous egg matrix in *Rotylenchulus* species flows from the vulva (Fig. 3) and it is produced by vaginal glands (Sivakamur and Seshadri, 1971), in contrast to gelatinous matrix production by rectal glands in *Meloidogyne* species. The number of eggs found in an egg mass usually does not exceed 60 but can reach 200 (Sivakumar and Seshadri, 1971). Males are not parasitic (Fig. 2C).

The timing of developmental events varies with species, as well as with temperature (Bird, 1984; Heald and Inserra, 1988;

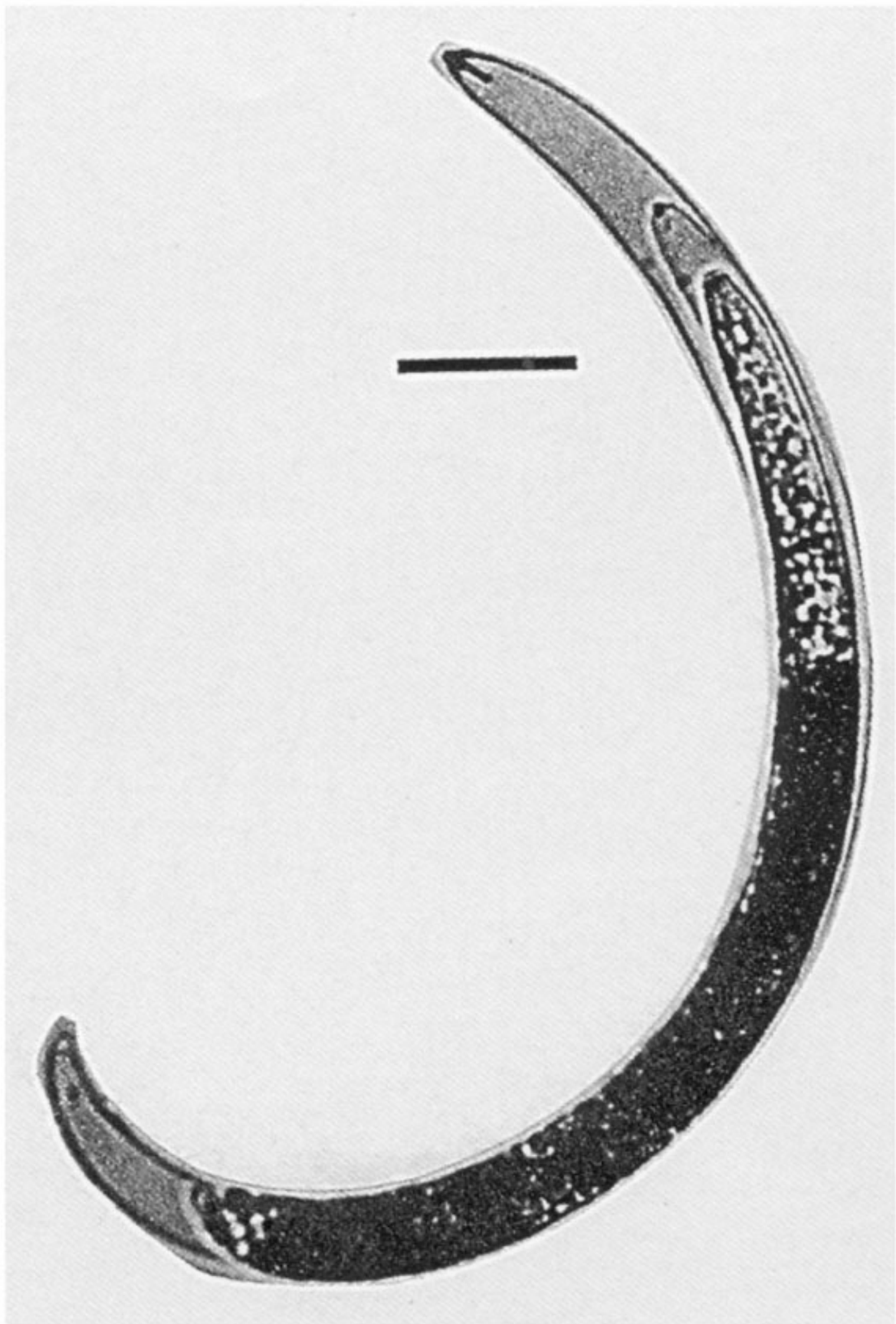


Fig. 1. Fourth-stage juvenile of *Rotylenchulus macrodoratus* enveloped by two cuticles. Scale bar = 34 μm . (After Inserra and Vovlas, 1980).

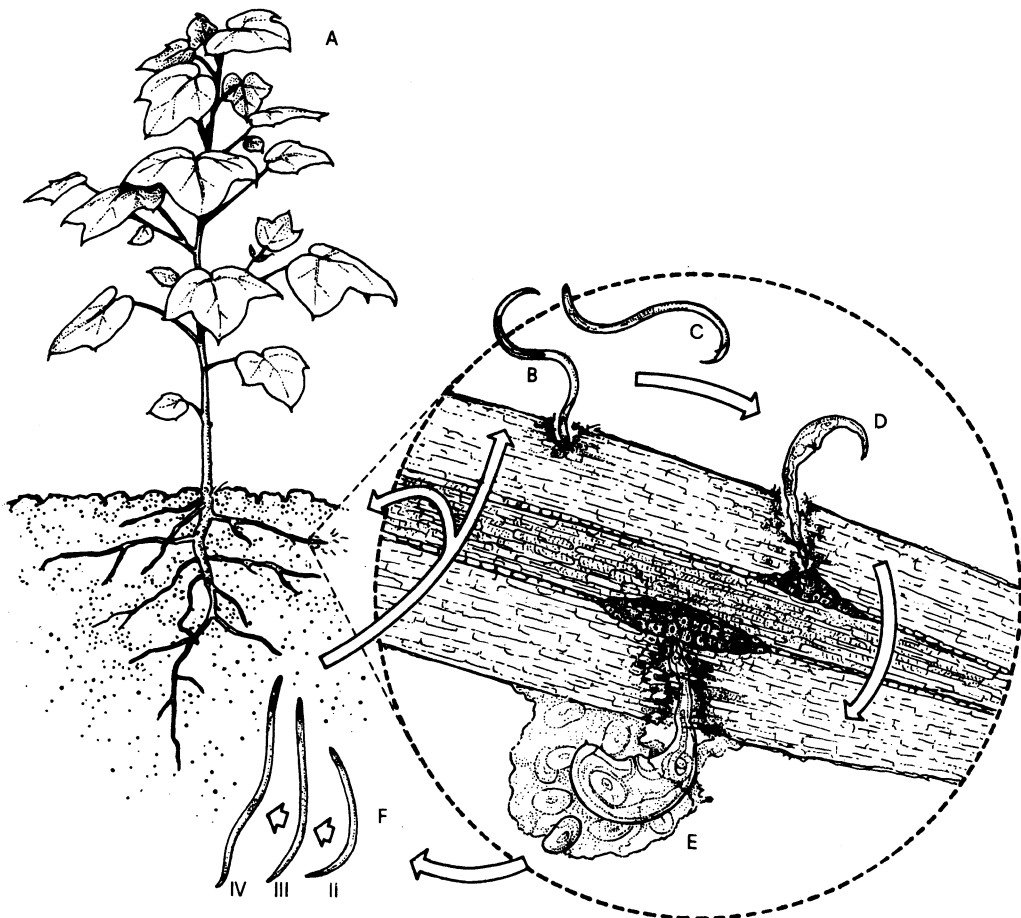


Fig. 2. Life cycle of *Rotylenchulus reniformis* on cotton. A) Cotton plant growing in soil infested by reniform nematodes. B) Immature vermiform female penetrating with the anterior portion of the body into a feeder root. C) Non-parasitic male. D) Female in more advanced stage of gonad maturation and establishing a permanent feeding site in the stele of the root. E) Mature female feeding on a stelar syncytium and producing eggs in the gelatinous matrix, which surrounds the swollen posterior portion of the body protruding from the root surface. F) Second, third, and fourth-stage juveniles in the soil.

Rebois, 1973) and host (Bishnoi and Yadav, 1989), but typically eggs hatch 1-2 weeks after being laid, and the infective stage is reached 1-2 weeks after hatch. Once root penetration occurs, 1 or 2 more weeks are required for females to reach reproductive maturity; in the absence of a host, however, vermiform stages in the soil can remain in a state of arrested development indefinitely. The life cycle can be

shorter than 3 weeks or can last more than 2 years if a host is not present and the soil remains dry. Additional details on the life cycle of *R. reniformis* are summarized by Gaur and Perry (1991b) and by Sivakumar and Seshadri (1971).

Identification: *Rotylenchulus* species belong to the subfamily Rotylenchulinae, in the family Hoplolaimidae. Identification of the genus is based mainly on mor-

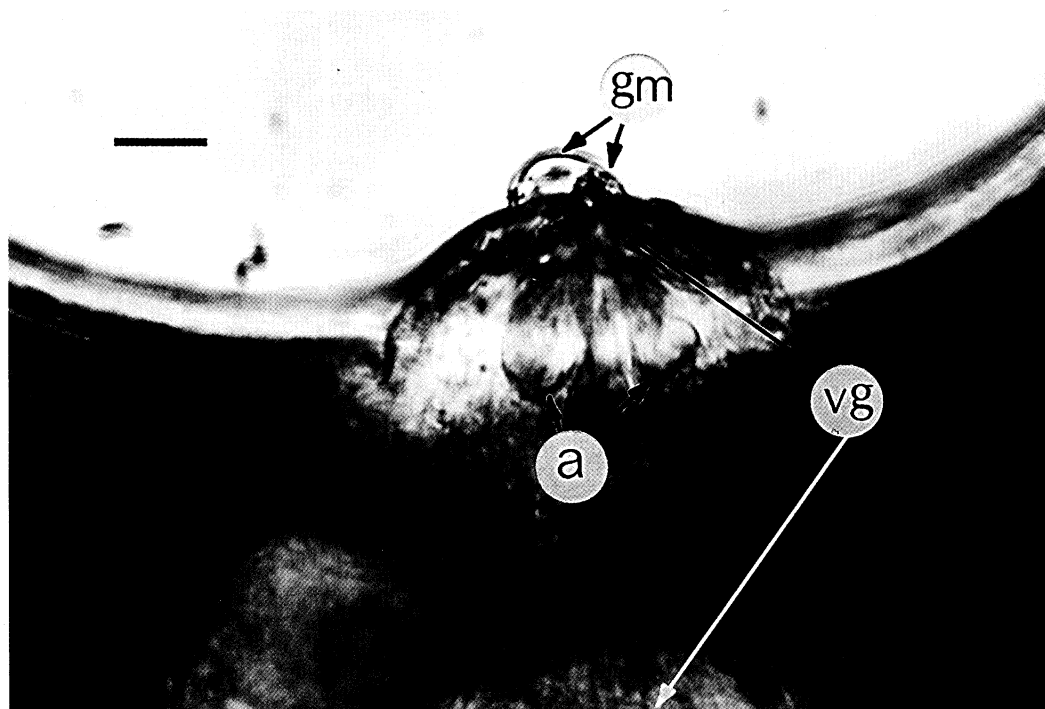


Fig. 3. *Rotylenchulus reniformis* mature female. Lateral view of the vulval area showing two droplets of gelatinous matrix (gm) flowing from the vulva (not visible in lateral view). Note the ampullae (a) where the gelatinous matrix secreted by the vaginal glands (not visible) accumulates. vg = vagina. Scale bar = 7 μ m.

phological characters of vermiform females (Fig. 4). Morphological characters of swollen females and the presence or absence of males are useful for the separation of *Rotylenchulus* species. A simple key to the species of *Rotylenchulus* was proposed by Germani (1978a). We provide a modified version of this key.

Key to the species of the genus Rotylenchulus based on morphological characteristics of immature females.[†]

1. Stylet > 27 μ m *R. sacchari*

- Stylet = 10-15 μ m 2
- Stylet = 16-26 μ m (males present) 5
- 2. Males present 3
- Males absent or rare 4
- 3. V = 55-66% *R. borealis*
- V = 67-72% *R. anamictus*
- 4. Head conoid, truncate *R. leptus*
- Head rounded *R. parvus*
- 5. V = 55-63% 6
- V > 63% 7
- 6. Tail with clavate terminus
 *R. clavicaudatus*
- Tail with bluntly rounded terminus
 *R. macrosoma*

[†]*Rotylenchulus brevitubulus* is omitted from the key because second-stage juveniles of this species have a bifurcate tail terminus completely unlike other *Rotylenchulus* spp. Furthermore, in *R. brevitubulus* vermiform females the distance between the dorsal esophageal gland orifice and the base of stylet knobs is shorter (<10 μ m) than that (>10 μ m) of other *Rotylenchulus* species.

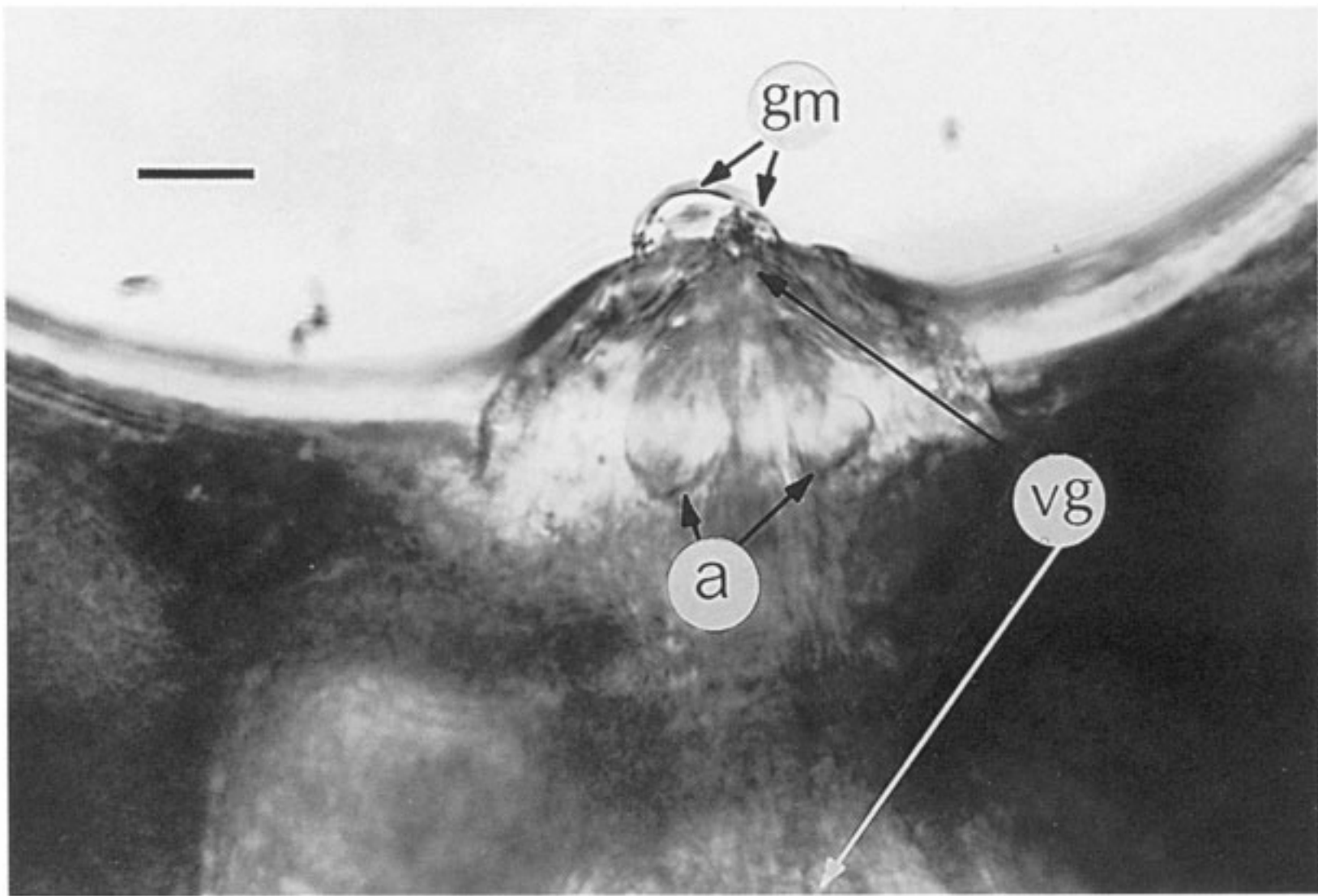


Fig. 3. *Rotylenchulus reniformis* mature female. Lateral view of the vulval area showing two droplets of gelatinous matrix (gm) flowing from the vulva (not visible in lateral view). Note the ampullae (a) where the gelatinous matrix secreted by the vaginal glands (not visible) accumulates. vg = vagina. Scale bar = 7 μ m.

Distance of dorsal esophageal gland orifice from stylet knobs

Stylet length

Shape and annulation of the lip region

Length of hyaline portion of the tail

Vulva position (V%)

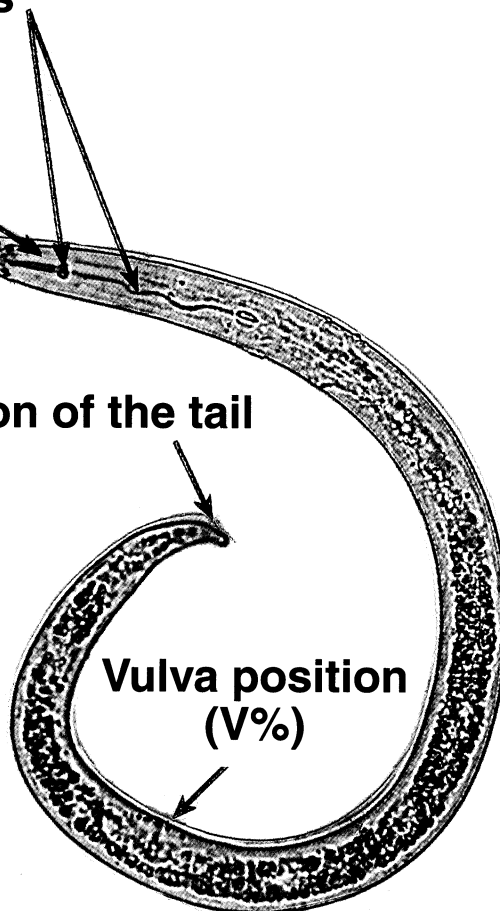


Fig. 4. Illustration of a *Rotylenchulus reniformis* immature female showing the major morphological characters of diagnostic value for separating *Rotylenchulus* species.

7. Stylet = 16-21 μm *R. reniformis*
 Stylet = 22-26 μm *R. macrodoratus*

Vermiform females of *R. anamictus*, *R. borealis*, *R. leptus*, and *R. parvus* have a shorter stylet (15 μm or less) than that (16 μm or more) of *R. clavicaudatus*, *R. macrodoratus*, *R. macrosoma*, and *R. reniformis*. However, populations of *R. borealis* with a stylet length of 16 μm have been reported from The Netherlands. For these populations

other morphological characters of diagnostic value, such as the position of the vulva, which is more anterior ($V = 57-60\%$) than in *R. reniformis*, should be used. Dasgupta *et al.* (1968) proposed the separation of *Rotylenchulus* species into five groups differing in the shape of the lip region and length of the hyaline portion of the tail (Fig. 5).

Parasitic habits and pathology: Information on parasitic habits of reniform nematodes and the pathology caused by them is

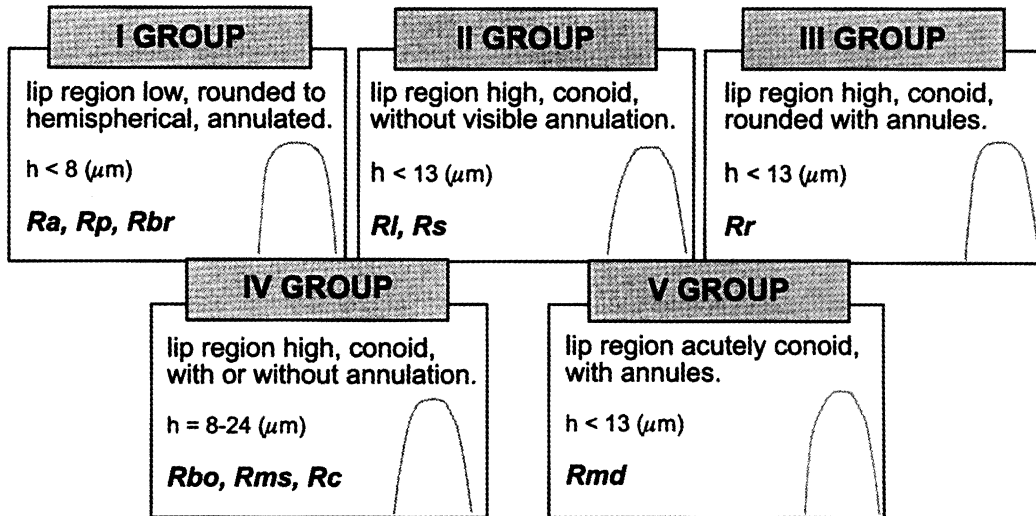


Fig. 5. Morphological groups of species, based on lip morphology and length of hyaline portion of tail (h), proposed by Dasgupta *et al.*, 1968 and updated in 1996 for the genus *Rotylenchulus*. *Ra* = *R. anamictus*, *Rbo* = *R. borealis*, *Rbr* = *R. brevitubulus*, *Rc* = *R. clavicaudatus*, *Rl* = *R. leptus*, *Rmd* = *R. macrodoratus*, *Rms* = *R. macrosoma*, *Rp* = *R. parvus*, *Rr* = *R. reniformis*, and *Rs* = *R. sacchari*.

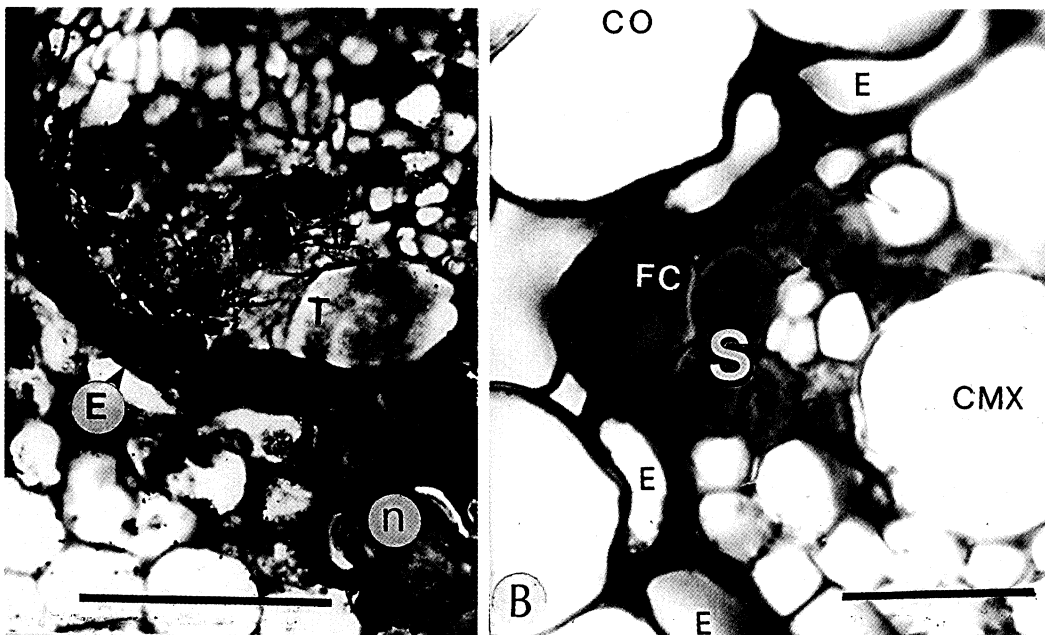


Fig. 6. Trophic sites induced by reniform nematode species. A) Cross section of a *Vitis vinifera* root showing a *Rotylenchulus macrodoratus* female (*n*) with the stylet inserted through the wall of an endodermal cell (*E*) and initiating the formation of a trophic site (uninucleate giant cell) (*T*) in the stele. B) Cross section of a *Zea mays* root showing a trophic site (stelar syncytium) (*S*) induced by *Rotylenchulus borealis*. Note the syncytium expanding from a feeding cell (*FC*) adjacent to the endodermis (*E*) in the pericycle and vascular parenchyma. *CO* = cortical parenchyma. *CMX* = metaxylem element. Scale bars = 50 μm in A and 25 μm in B. (After Inserra and Vovlas, 1980; Vovlas and Inserra, 1982).

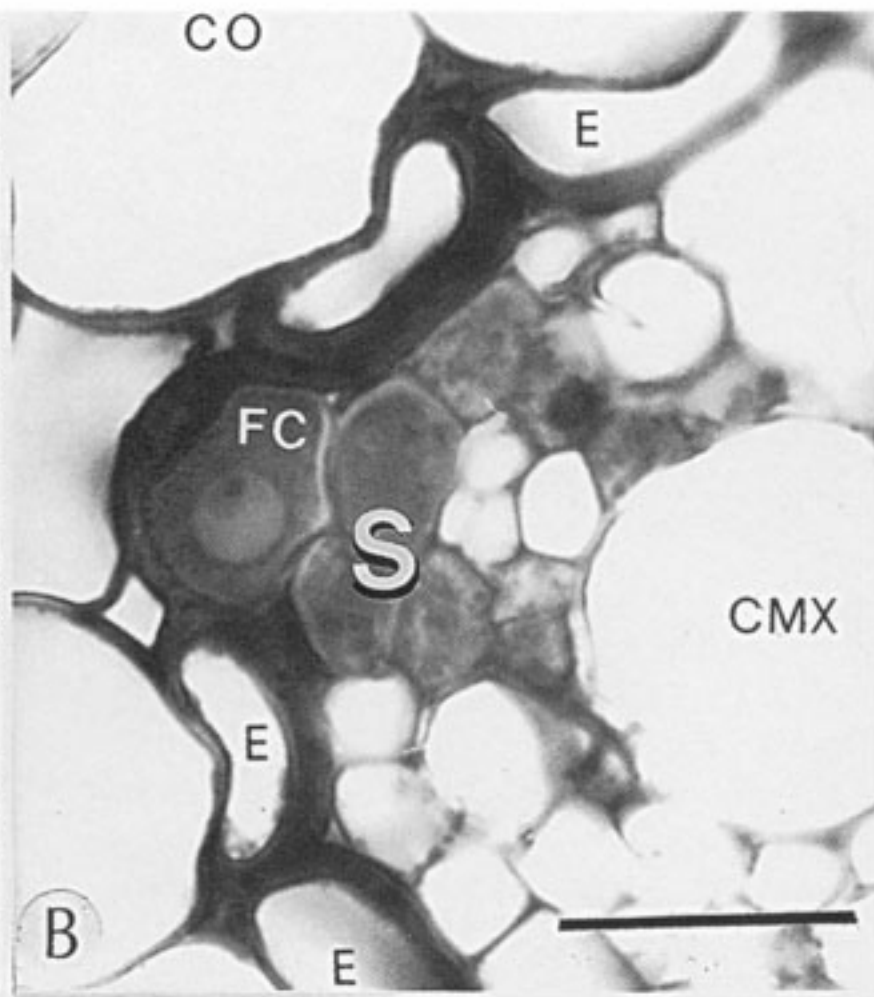
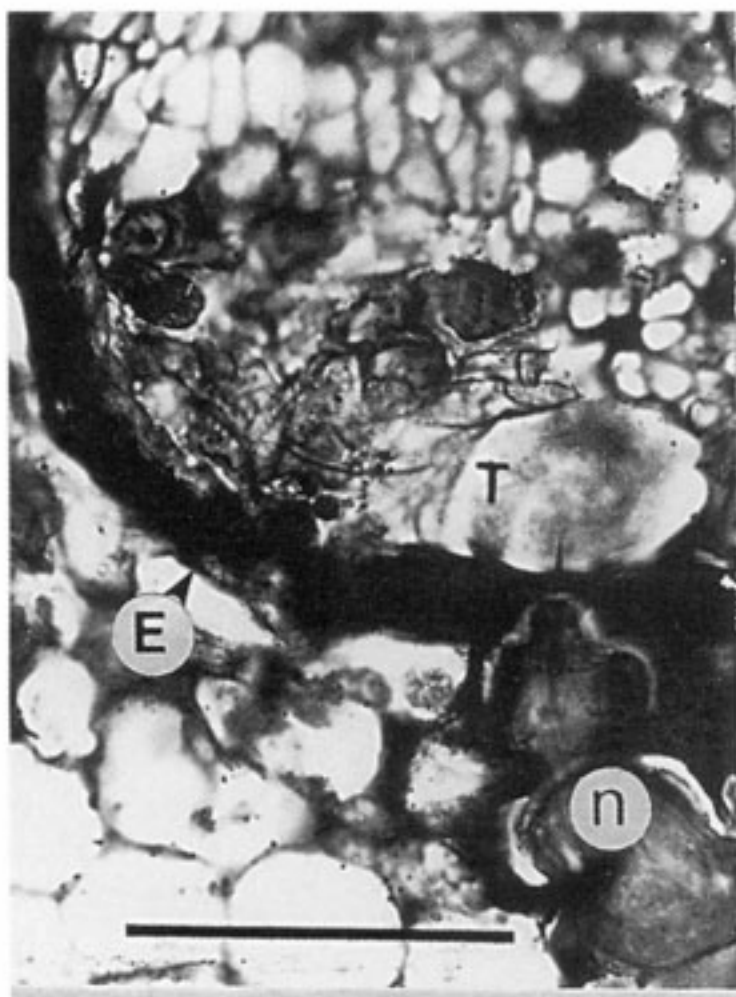


Fig. 6. Trophic sites induced by reniform nematode species. A) Cross section of a *Vitis vinifera* root showing a *Rotylenchulus macrodoratus* female (n) with the stylet inserted through the wall of an endodermal cell (E) and initiating the formation of a trophic site (uninucleate giant cell) (T) in the stele. B) Cross section of a *Zea mays* root showing a trophic site (stelar syncytium) (S) induced by *Rotylenchulus borealis*. Note the syncytium expanding from a feeding cell (FC) adjacent to the endodermis (E) in the pericycle and vascular parenchyma. CO = cortical parenchyma. CMX = metaxylem element. Scale bars = 50 μ m in A and 25 μ m in B. (After Inserra and Vovlas, 1980; Vovlas and Inserra, 1982).

available for only five of the ten species. The histopathological changes they induce have been studied in numerous plants by observing serial sections of root tissue under the transmission electron or compound light microscope. *Rotylenchulus borealis* has been studied on both *Ipomoea batatas* and *Zea mays* (Fig. 6B) (Vovlas and Inserra, 1982; Vovlas *et al.*, 1985), *R. macrosoma* on *Glycine max* (Cohn and Mordechai, 1988), *R. parvus* on *S. officinarum*

(Vovlas *et al.*, 1985), and *R. macrodoratus* on seven hosts, including *Dianthus barbatus* (Inserra and Vovlas, 1980), *Ficus carica* (Fig. 7A) (Inserra and Vovlas, 1980), *G. max* (Cohn, 1976), *Olea europaea* (Fig. 7B) (Vovlas and Inserra, 1976), *Pistacia vera* (Fig. 7C) (Vovlas, 1983), *Quercus calliprinos* (Cohn, 1976), and *Vitis vinifera* (Fig. 6A) (Vovlas and Vlachopoulos, 1991). Other histopathological studies have examined *R. reniformis* on more than 20 crop species,

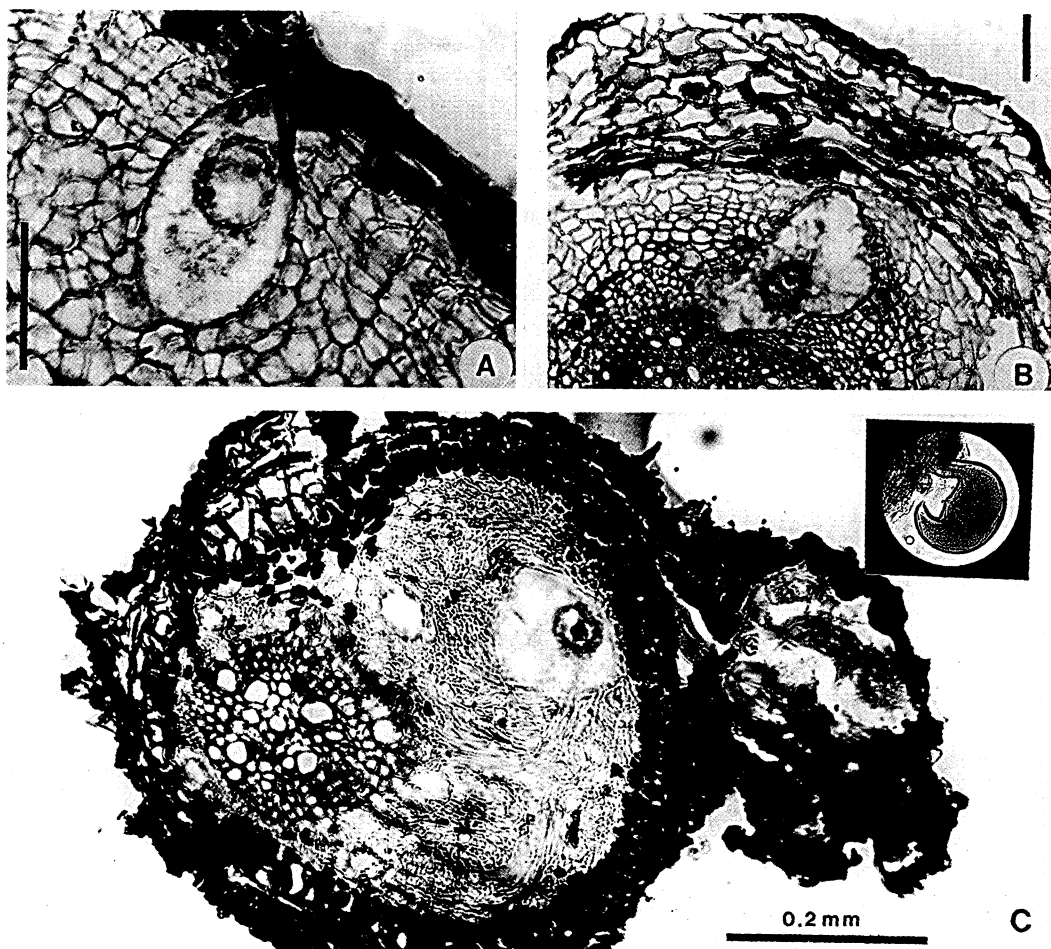


Fig. 7. Trophic sites induced by *Rotylenchulus macrodoratus*. Nematode-infected cross sections of *Ficus carica* (A), *Olea europaea* (B), and *Pistacia vera* (C) roots showing an uninucleate giant cell with hypertrophied nucleus and prominent nucleolus in the stele. Scale bars in A and B = 50 μ m. (After Inserra and Vovlas, 1980; Vovlas, 1983).

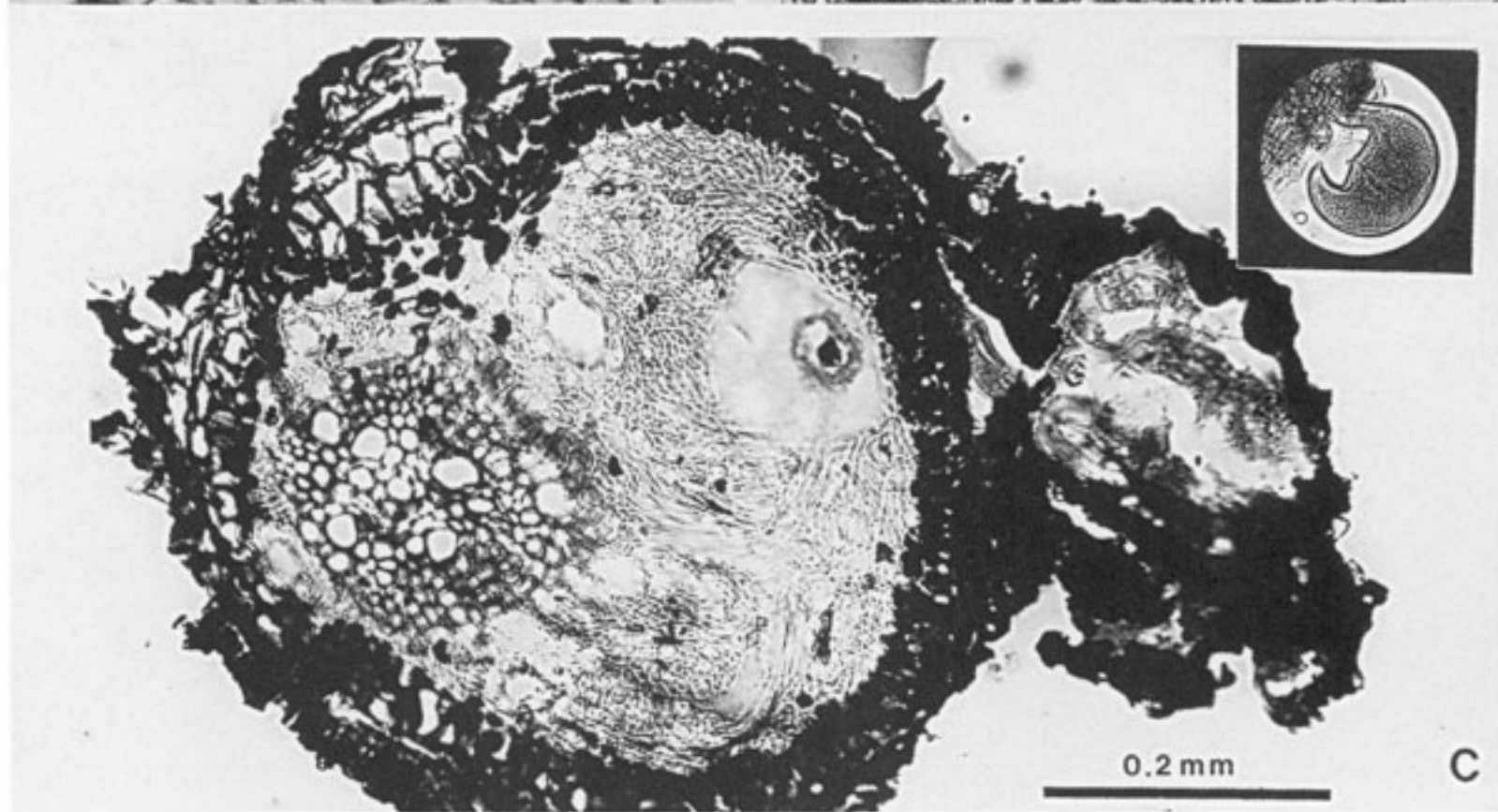
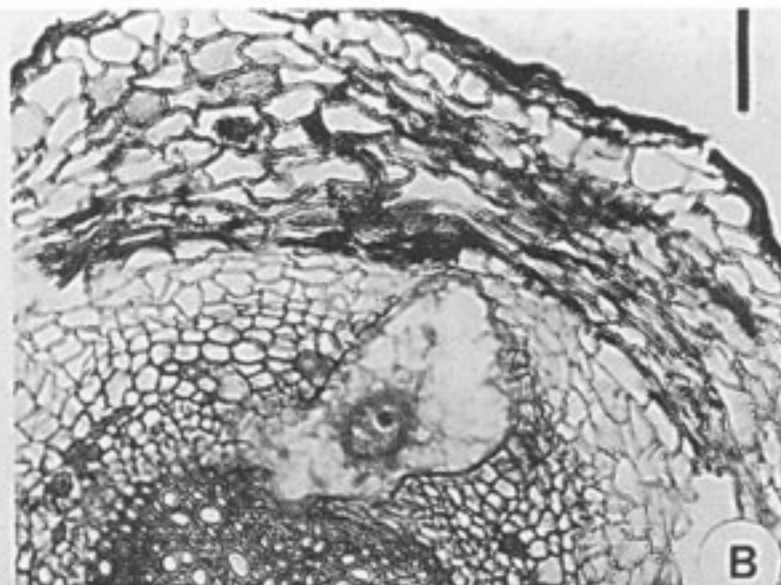
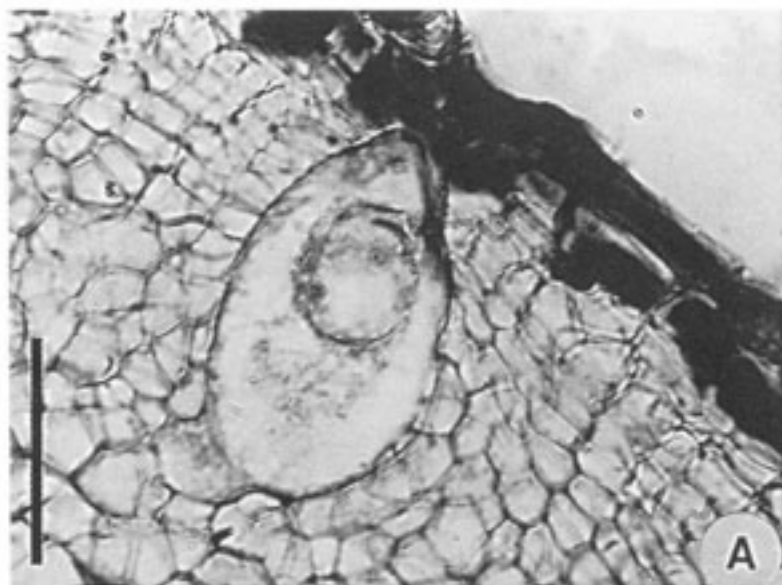


Fig. 7. Trophic sites induced by *Rotylenchulus macrodoratus*. Nematode-infected cross sections of *Ficus carica* (A), *Olea europaea* (B), and *Pistacia vera* (C) roots showing an uninucleate giant cell with hypertrophied nucleus and prominent nucleolus in the stele. Scale bars in A and B = 50 μ m. (After Inserra and Vovlas, 1980; Vovlas, 1983).

including *Brassica oleracea* var. *botrytis* (Khan and Khan, 1985), *Carica papaya* (Sivakumar and Seshadri, 1972), *Coffea arabica* (Vovlas and Lamberti, 1990), *Cucumis melo* var. *cantalupensis* (Heald, 1975; Heald *et al.*, 1988), *Cucumis sativus* (Birchfield, 1972), *G. max* (Cohn, 1976; Farahat and Kheir, 1983; Jones and Dropkin, 1975; Meredith *et al.*, 1983; Rebois *et al.*, 1975), *Gossypium hirsutum* (Birchfield, 1962; Cohn, 1973, Cohn, 1976; Rebois, 1980), *Helianthus annuus* (Robinson and Orr, 1980), *I. batatas* (Birchfield, 1972), *Lycopersicon esculentum* (Cohn, 1973; Khan *et al.*, 1985; Sivakumar and Seshadri, 1972), *Mentha* sp. (Cohn, 1973, 1976), *Musa acuminata* (Fig. 8A-C) (Vovlas and Ekanayake, 1985), *Nicotiana tabacum* (Patel, 1986; Patel *et al.*, 1988), *Passiflora edulis* f. sp. *flavicarpa* (Suárez *et al.*, 1993), *Phaseolus vulgaris* (Birchfield, 1972; Farahat and Kheir, 1983), *Pisum sativum* (Farahat and Kheir, 1983), *Ricinus communis* (Sivakumar and Seshadri, 1972), *S. officinarum* (Birchfield, 1972), *Trifolium alexandrinum* (Massoud and Gharob, 1988), *Vigna unguiculata* (Birchfield, 1972; Razak and Evans, 1976;

Taha and Kassab, 1979), *V. vinifera* (Taha and Sultan, 1979), *Washingtonia robusta* (Inserra *et al.*, 1994), and *Z. mays* (Birchfield, 1972).

The host responses induced by different *Rotylenchulus* species are not necessarily identical on the same host, and histological responses to a single species can differ somewhat among plant species. However, some generalizations can be made, realizing that exceptions do occur. During root invasion, the anterior portion of the body of the vermiform female penetrates the epidermis and cortical parenchyma of the root and usually stops to feed permanently on a single endodermal cell (Fig. 6A). This results in the formation of a trophic site. Except for *R. macrodoratus*, the trophic site usually consists of a stelar syncytium, which originates from an endodermal cell and enlarges by incorporating a curved sheet of cells in the pericycle, vascular parenchyma, and sometimes phloem, through partial dissolution of common cell walls (Fig. 6B). Syncytial cells have densely staining granular cytoplasm and enlarged nuclei, and are slightly hypertrophied

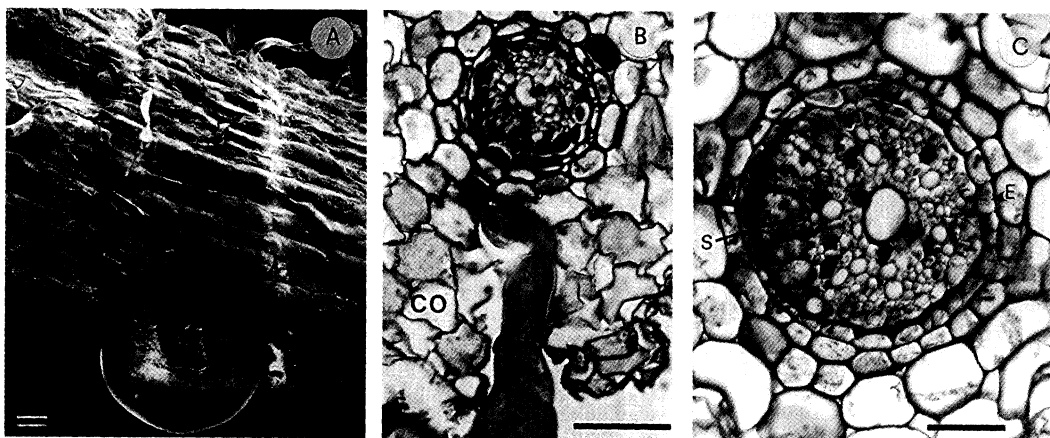


Fig. 8. Anatomical alterations induced by *Rotylenchulus reniformis* on *Musa acuminata* roots. A) Root infected by a swollen female. B) Female (N) partially penetrated into the cortical parenchyma (CO). C) Syncytium (S) induced by nematode feeding activity and expanded from the endodermis (E) into the pericycle and vascular parenchyma. Scale bars for all figures = 50 μ m. (After Vovlas and Ekanayake, 1985).

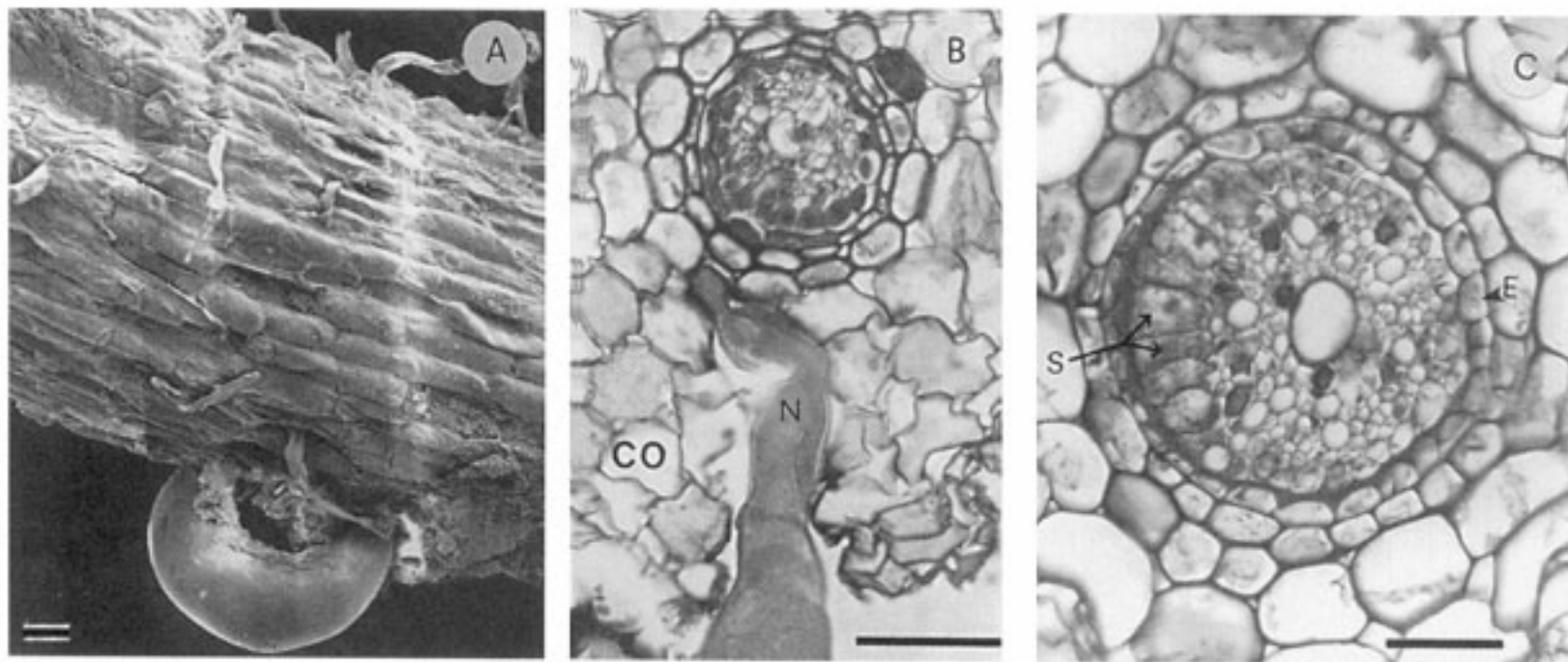


Fig. 8. Anatomical alterations induced by *Rotylenchulus reniformis* on *Musa acuminata* roots. A) Root infected by a swollen female. B) Female (N) partially penetrated into the cortical parenchyma (CO). C) Syncytium (S) induced by nematode feeding activity and expanded from the endodermis (E) into the pericycle and vascular parenchyma. Scale bars for all figures = 50 μm . (After Vovlas and Ekanayake, 1985).

(Rebois *et al.*, 1975; Vovlas and Inserra, 1982; Vovlas *et al.*, 1985) (Figs. 6B; 8B,C). In all seven hosts examined so far, the trophic site induced by *R. macrodorum* consisted of an hypertrophied, uninucleate giant cell of endodermal origin (Cohn, 1976; Cohn and Mordechai, 1977; Inserra and Vovlas, 1980) (Fig. 7A-C). Specialized feeding sites typically do not differ appreciably among plant-parasitic nematodes within the same genus. *Rotylenchulus* appears to be an exception since *R. macrodorum* induces a uninucleate giant cell, while other species (*R. borealis*, *R. macrosoma*, *R. parvus*, and *R. reniformis*) induce a syncytium in the stele of host roots (Fig. 9). In various concomitant infections of plant roots by *R. reniformis* and other sed-

entary nematodes, the characteristic plant response to each species occurred as if the other nematode species were absent (Heald *et al.*, 1988; Jones and Dropkin, 1975; Massoud and Ghorab, 1988; Patel *et al.*, 1988; Taha and Kassab, 1979; Vovlas and Ekanayake, 1985).

A temporal study of infection by *R. reniformis* on resistant and susceptible soybean with the transmission electron microscope revealed that syncytial development in susceptible plants went through two phases: 1) an initial phase involving partial cell wall lysis and separation, and 2) an anabolic phase characterized by organelle proliferation and secondary wall deposits (Rebois *et al.*, 1975). In resistant plants, the initial phase was accelerated, resulting in

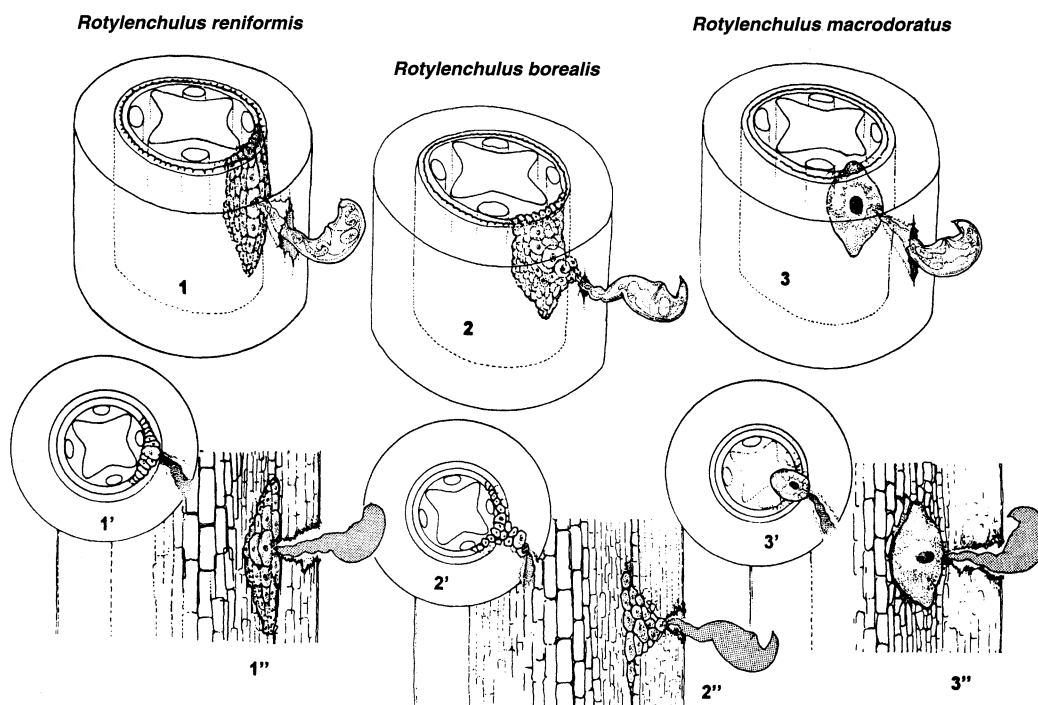


Fig. 9. Schematic representation in tridimensional (1-3), transversal (1'-3'), and longitudinal (1''-3'') view of trophic sites induced by reniform nematode species. Note the uninucleate giant cell (3, 3', and 3'') induced by *Rotylenchulus macrodorum* compared to the syncytium, which is the most common host response caused by *Rotylenchulus* species including *R. reniformis* (1, 1', and 1'') and *R. borealis* (2, 2', and 2'').

cell lysis and thus failure to enter the anabolic phase. A similar response has been reported for the old world cotton species, *Gossypium arboreum* (Carter, 1981b).

ROTYLENCHULUS RENIFORMIS

Rotylenchulus reniformis (Figs. 10, 11) is the *Rotylenchulus* species of greatest economic importance. Excellent reviews on its biology, systematics, distribution, eco-

nomical impact, and management are given by Varaprasad (1986) and Gaur and Perry (1991b). We will briefly discuss and update the geographical distribution and economic impact of *R. reniformis* but will focus on host range, immune species, sources of resistance in crop plants, and opportunities for crop rotation.

Geographical distribution: *Rotylenchulus reniformis* has been found in association

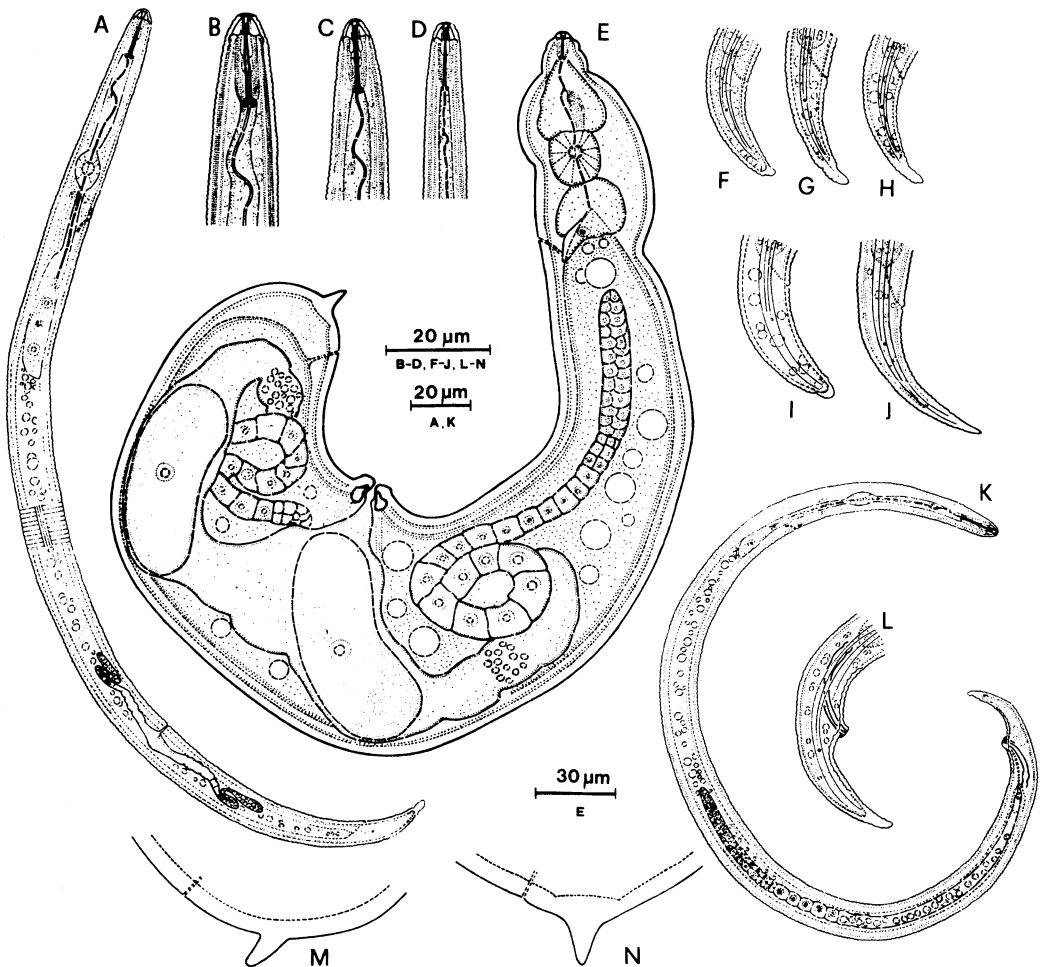


Fig. 10. *Rotylenchulus reniformis* life stages. A) Immature female. B) Anterior portion of the body of immature female. C) Anterior portion of the body of juvenile. D) Anterior portion of the body of male. E) Mature female. F-I) Tail of immature female. J) Tail of juvenile. K) Male. L) Tail of male. M, N) Tail of mature female. (After Dasgupta *et al.*, 1968, modified).

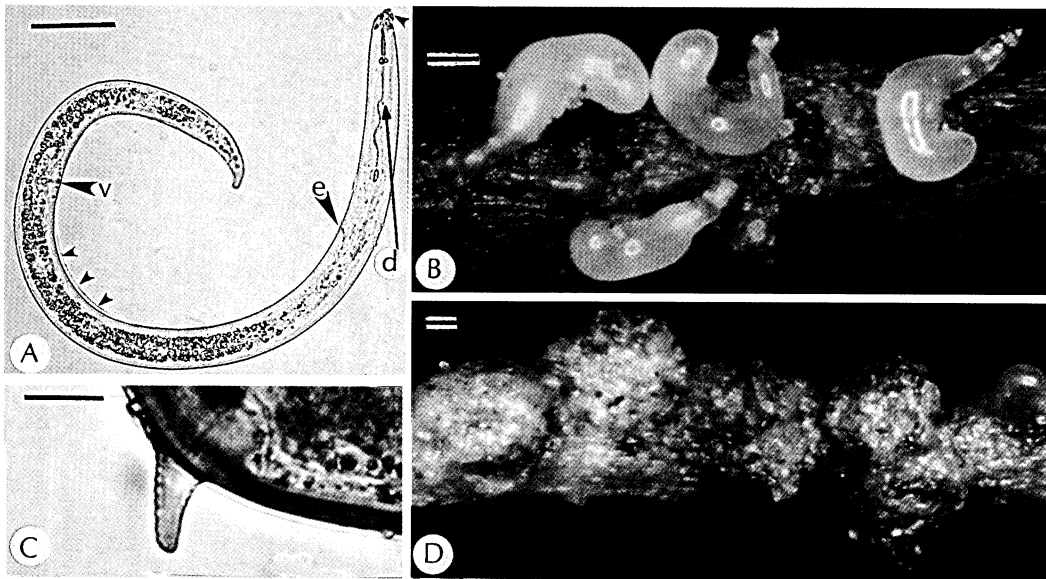


Fig. 11. Selected life stages of *Rotylenchulus reniformis*. A) Immature female enclosed in the cuticles (indicated by small arrow heads) of juvenile stages. d = dorsal esophageal gland orifice; e = excretory pore; v = vulva. B) *Gossypium* sp. feeder root infected by swollen females artificially detached from the root tissues. C) Posterior portion of the body of a swollen female showing the characteristic spike-like terminus. D) Egg masses attached to a cotton feeder root. Scale bars = 32 μ m in A, 110 μ m in B and D, and 8 μ m in C. (Photos B and D courtesy of C. Overstreet).

with hundreds of crop and native plants in tropical, subtropical, and warm temperate regions in thousands of localities in South America, Central America, North America, the Caribbean Basin, Africa, southern Europe (Malta and Spain only), the Middle East, India, Southeast Asia, Australasia, the Indian Ocean, China, Japan, the Philippines, and the Pacific. Its wide distribution likely resulted from an exceptionally wide host range (Table 2) and an ability to survive extended periods in a dehydrated state (Birchfield and Martin, 1967; Gaur and Perry, 1991a; Heald and Inserra, 1988; Inserra and Dunn, 1992; Radewald and Takeshita, 1964; Rodriguez-Fuentes, 1980; Sehgal and Gaur, 1988, 1989; Tsai and Apt, 1979; Womersley and Ching, 1989). Anhydrobiotic *R. reniformis* are dispersed long distances in dust storms (Gaur, 1988).

Host range: Several extensive host lists and numerous new host records for *R. reni-*

formis have been published (Table 2). The reliability of original host records varies greatly, as do the criteria used to assign host status. Authors of host lists often have listed previous reports of *R. reniformis* from soil samples taken near a suspected host, separate from reports that confirmed reproduction by directly observing mature females and eggs, or that confirmed reproduction by monitoring population increases in pot experiments. Even so, in many cases the wording of a report is not clear enough to know precisely what was and was not observed. In other cases, *R. reniformis* was assumed to be the *Rotylenchulus* species present or the authors stated that the species was not determined.

Thorne (1961) predicted that hundreds of hosts for *R. reniformis* would be found. In our examination of the literature, we found reports of reproduction by *R. reniformis* on 314 of 364 plant species

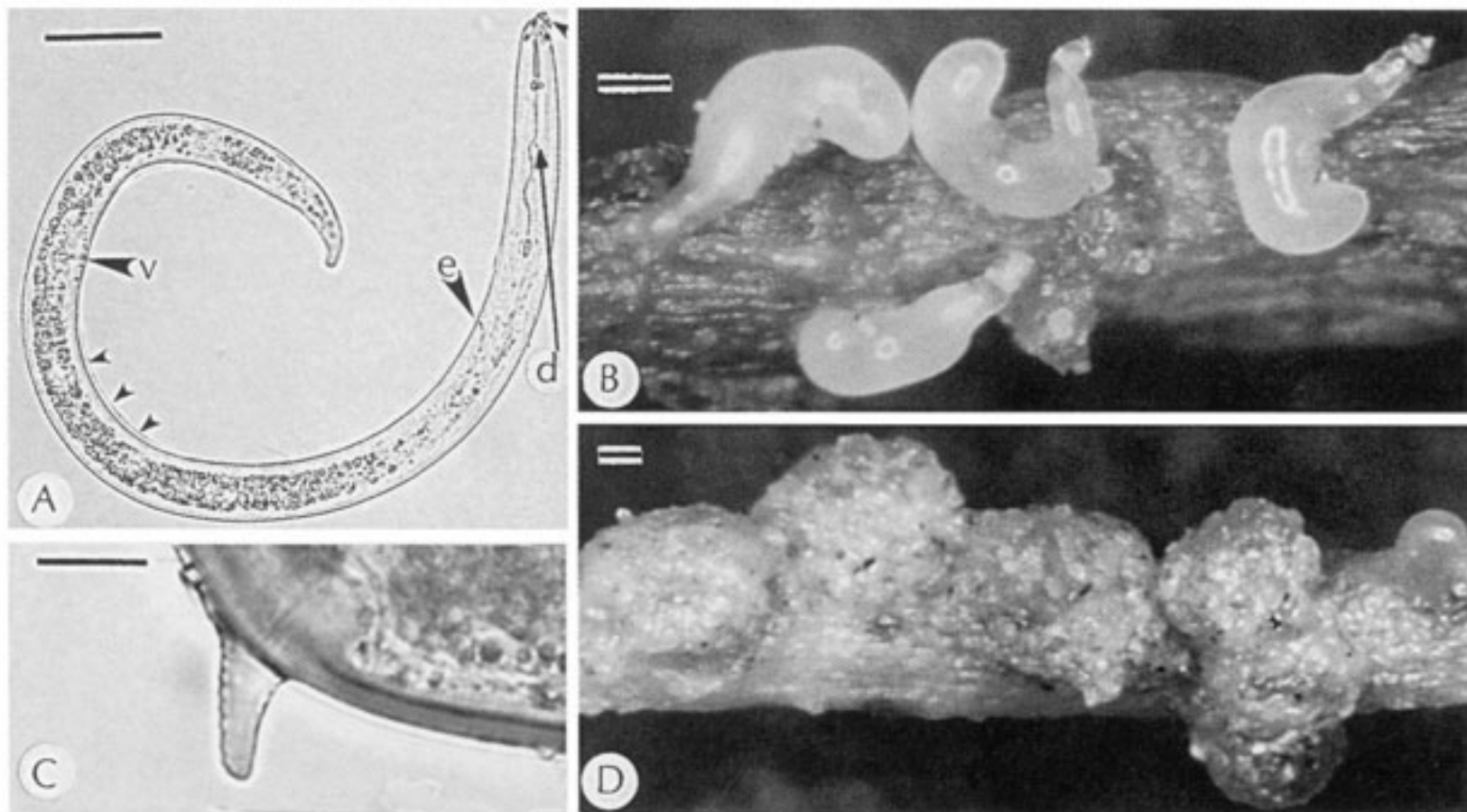


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Table 2. Reported hosts and nonhosts for *Rotylenchulus reniformis* according to numeric literature references as footnoted.

	<i>Abelmoschus esculentus</i> (L.) Moench	12, 44, 49, 56, 73, 104	<i>Averrhoa carambola</i> L.	46
	<i>Abutilon theophrasti</i> Medic.	104	<i>Begonia semperflorens</i> Link & Otto	56
	<i>Acalypha arvensis</i> Poepp. & Endl	76	<i>Benincasa hispida</i> (Thumb.) Cogn.	44
	<i>Acoelorthaps wrightii</i> (Griseb. & H. Wendl.) H. Wendl. ex Becc.	41	<i>Beta vulgaris</i> L.	12, 56
	<i>Adansonia digitata</i> L.	96	<i>Bidens pilosa</i> L.	38, 76, 92
	<i>Aeschynomene americana</i> L.	38, 76	NH <i>Bismarckia nobilis</i> Hildebr. & H. Awend.	41
	<i>Aeschynomene virginica</i> (L.) BSP	14	<i>Bixa orellana</i> L.	56
	<i>Ageratum conyzoides</i> L.	51, 56, 76	<i>Blumea hieracifolia</i> DC.	51
H/NH	<i>Allium cepa</i> L.	12, 15, 47, 87	<i>Bracharia mutica</i> (Forsk.) Stapf	86
H/NH	<i>Allium sativum</i> L.	45, 87, 92	<i>Brassica napus</i> L.	92
	<i>Aloe vera</i> (L.) Brum. f.	R. N. Inseerra, 1997	<i>Brassica nigra</i> (L.) W. D. J. Koch	12, 44
	<i>Amaranthus dubius</i> Mart. ex Thell.	76	<i>Brassica oleracea</i> L. <i>acephala</i> group	56
	<i>Amaranthus spinosus</i> L.	38, 51, 76	<i>Brassica oleracea</i> L. <i>botrytis</i> group	56
H/NH	<i>Amaranthus viridis</i> L.	35, 51, 92	<i>Brassica oleracea</i> L. <i>capitata</i> group	47, 56
	<i>Ananas comosus</i> (= <i>sativus</i>) (L.) Merrill	50, 56, 82, 83	<i>Brassica rapa</i> L.	12, 47, 56
NH	<i>Anethum graveolens</i> L.	45, 47	<i>Brassica rapa</i> L. <i>pekinensis</i> group	56
	<i>Annona squamosa</i> L.	46	<i>Buddleia asiatica</i> Lour.	56
	<i>Anoda cristata</i> (L.) Schlechtend	104	<i>Caesalpinia</i> (= <i>Poinciana</i>) <i>pulcherrima</i> (L.) SW.	73, 74
	<i>Arachis hypogaea</i> L.	12	<i>Cajanus acutifolius</i> (F. Muell.) Maesen	84
NH	Archontophoenix alexandre	41	[= <i>Alyosia acutifolia</i> (F. Muell. ex Benth) Reynolds & Peley]	
NH	<i>Areca catechu</i> L.	50	<i>Cajanus albicans</i> (W. & A.) Maesen (= <i>Cantharosperma albicans</i> Wight & Am.)	84
	<i>Argemone mexicana</i> L.	92	<i>Cajanus cajan</i> (L.) Millsp.	56, 87
	<i>Argyrea nervosa</i> (Burm. f.) Bojer	56	<i>Cajanus cajanifolius</i> (Haines) Maesen (= <i>Alyosia cajanifolia</i> Haines)	84
	<i>Artemisia vulgaris</i> L.	76	<i>Cajanus goensis</i> Dalz. ex Hook. (= <i>Alyosia barbata</i> Barker ex Hook.)	84
	<i>Ariticum lappa</i> L.	70	<i>Cajanus grandifolius</i> (Benth. ex Baker) Maesen (= <i>Alyosia grandifolia</i> Benth. ex Hook.)	84
	<i>Artocarpus altiss</i> (Parkins.) Fosb.	21		
	<i>Artocarpus heterophyllus</i> Lam.	46		
	<i>Asphodelus fistulosus</i> (= <i>tenyfilolius</i>) L.	51		
NH	<i>Avena sativa</i> L.	12		

Table 2. (Continued) Reported hosts and nonhosts for *Rotylenchulus reniformis* according to numeric literature references as footnoted.

	<i>Colocasia esculenta</i> (L.) Schott	64	<i>Desmodium tortuosum</i> (Sw.) DC.	19
	<i>Commelina diffusa</i> Burm. f.	38, 76	<i>Dichanthium annulatum</i> (Forsk.) Stapf	46
	<i>Commelina erecta</i> (L.) Chev. (= <i>elegans</i> HBK.)	86	<i>Digitaria eriantha</i> Steud. (= <i>decumbens</i> Stent.)	18
	<i>Convolvulus arvensis</i> L.	51	<i>Digitaria sanguinalis</i> (L.) Scop.	14
	<i>Conyza bonariensis</i> (L.) Cronq. [= <i>Erigeron albidus</i> (Willd.) Gray]	56	<i>Dioscorea polygonoides</i> Humb. & Bonpl. ex Willd.	92
	<i>Cordylone fruticosa</i> (L.) Chev. [= <i>terminalis</i> (L.) Kunth]	5	<i>Dioscorea rotundata</i> Poir.	2
	<i>Coronopus didymus</i> (L.) Sm.	51	<i>Echeveria</i> sp.	56
NH	<i>Crotalaria breviflora</i> DC.	89	H/NH <i>Echinochloa crus-galli</i> (L.) Beauv.	12, 14
H/NH	<i>Crotalaria juncea</i> L.	18, 73, 89	<i>Elettaria cardamomum</i> (L.) Maton	50
NH	<i>Crotalaria lanceolata</i> E. Mey.	89	<i>Eleusine indica</i> (L.) Gaertn.	67, 76
H/NH	<i>Crotalaria pallida</i> Aiton var. <i>obovata</i> (G. Don) Polhill (= <i>C. mucronata</i> Desv.)	73, 89	<i>Emblia officinalis</i> (<i>Phyllanthus emblica</i> L.)	46
	<i>Crotalaria spectabilis</i> Roth	56, 89	<i>Emilia coccinea</i> (Sims) G. Don	86
NH	<i>Crotalaria virgulata</i> Klotzsch. ssp. <i>gramiana</i> (Harvey) Polhill	89	<i>Emilia fosbergii</i> D. H. Nicolson	76
	<i>Cucumis melo</i> L.	12, 34, 44	<i>Emilia sonchifolia</i> (L.) DC.	56
	<i>Cucumis sativus</i> L.	12, 44, 47, 56	<i>Emilia sonchifolia</i> (L.) var. <i>javanica</i> (Burm.f.) Mattf.	53
	<i>Cucurbita maxima</i> Duchesne ex Lam.	6	<i>Eragrostis pilosa</i> (L.) Beauv.	51
	<i>Cucurbita moshata</i> (Duchesne) Poir.	44, 92	<i>Erechtites valerianaeifolia</i> (Spreng.) DC.	56
	<i>Cucurbita pepo</i> L.	12, 56	<i>Euphorbia heterophylla</i> (L.)	38, 59, 76
NH	<i>Cycas revoluta</i> Thunb	41	<i>Euphorbia milii</i> Des Moulins	26
	<i>Cynara scolymus</i> L.	56	<i>Euphorbia pulcherrima</i> Willd. ex Klotzsch	56
H/NH	<i>Cynodon dactylon</i> (L.) Pers.	12, 51, 87	<i>Ficus carica</i> L.	46
	<i>Cyperus esculentus</i> L.	65	<i>Ficus elastica</i> Roxb. ex Hornem.	90
H/NH	<i>Cyperus</i> (= <i>Torrulium</i>) <i>odoratus</i> L.	76, 86	<i>Fimbristylis miliacea</i> (L.) Vahl	86
H/NH	<i>Cyperus rotundus</i> L.	51, 86	<i>Flemingia macrophylla</i> Blume	84
NH	<i>Dactyloctenium aegyptiacum</i> Willd.	51	<i>Flemingia stricta</i> Wall.	84
H/NH	<i>Daucus carota</i> L.	12, 45, 56, 73, 74	<i>Flemingia strobilifera</i> (L.) Ait. & Ait.f.	84
			<i>Foeniculum vulgare</i> Mill	44
			<i>Galinsoga quadriradiata</i> (= <i>altata</i>) Ruiz & Pavon	38, 59, 76

Table 2. (Continued) Reported hosts and nonhosts for *Rotylenchulus reniformis* according to numeric literature references as footnoted.

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	<i>Convolvulus arvensis</i> L.	51	<i>Digitaria sanguinalis</i> (L.) Scop.	14
	<i>Conyza bonariensis</i> (L.) Cronq. [= <i>Erigeron albidus</i> (Willd.) Gray]	56	<i>Dioscorea polygonoides</i> Humb. & Bonpl. ex Willd.	92
	<i>Cordylone fruticosa</i> (L.) Chev. [= <i>terminalis</i> (L.) Kunth]	5	<i>Dioscorea rotundata</i> Poir.	2
	<i>Coronopus didymus</i> (L.) Sm.	51	<i>Echeveria</i> sp.	56
NH	<i>Crotalaria breviflora</i> DC.	89	H/NH <i>Echinochloa crus-galli</i> (L.) Beauv.	12, 14
H/NH	<i>Crotalaria juncea</i> L.	18, 73, 89	<i>Elettaria cardamomum</i> (L.) Maton	50
NH	<i>Crotalaria lanceolata</i> E. Mey.	89	<i>Eleusine indica</i> (L.) Gaertn.	67, 76
H/NH	<i>Crotalaria pallida</i> Aiton var. <i>obovata</i> (G. Don) Polhill (= <i>C. mucronata</i> Desv.)	73, 89	<i>Emblica officinalis</i> (<i>Phyllanthus emblica</i> L.)	46
	<i>Crotalaria spectabilis</i> Roth	56, 89	<i>Emilia coccinea</i> (Sims) G. Don	86
NH	<i>Crotalaria virgulata</i> Klotzsch. ssp. <i>gramiana</i> (Harvey) Polhill	89	<i>Emilia fosbergii</i> D. H. Nicolson	76
	<i>Cucumis melo</i> L.	12, 34, 44	<i>Emilia sonchifolia</i> (L.) DC.	56
	<i>Cucumis sativus</i> L.	12, 44, 47, 56	<i>Emilia sonchifolia</i> (L.) var. <i>javanica</i> (Burm.f.) Mattf.	53
	<i>Cucurbita maxima</i> Duchesne ex Lam.	6	<i>Eragrostis pilosa</i> (L.) Beauv.	51
	<i>Cucurbita moshata</i> (Duchesne) Poir.	44, 92	<i>Erechtites valerianaeifolia</i> (Spreng.) DC.	56
	<i>Cucurbita pepo</i> L.	12, 56	<i>Euphorbia heterophylla</i> (L.)	38, 59, 76
NH	<i>Cycas revoluta</i> Thunb	41	<i>Euphorbia milii</i> Des Moulins	26
	<i>Cynara scolymus</i> L.	56	<i>Euphorbia pulcherrima</i> Willd. ex Klotzsch	56
H/NH	<i>Cynodon dactylon</i> (L.) Pers.	12, 51, 87	<i>Ficus carica</i> L.	46
	<i>Cyperus esculentus</i> L.	65	<i>Ficus elastica</i> Roxb. ex Hornem.	90
H/NH	<i>Cyperus</i> (= <i>Torrulimum</i>) <i>odoratus</i> L.	76, 86	<i>Fimbristylis miliacea</i> (L.) Vahl	86
H/NH	<i>Cyperus rotundus</i> L.	51, 86	<i>Flemingia macrophylla</i> Blume	84
NH	<i>Dactyloctenium aegyptiacum</i> Willd.	51	<i>Flemingia stricta</i> Wall.	84
H/NH	<i>Daucus carota</i> L.	12, 45, 56, 73, 74	<i>Flemingia strobilifera</i> (L.) Ait. & Ait.f.	84
			<i>Foeniculum vulgare</i> Mill	44
			<i>Galinsoga quadriradiata</i> (= <i>altata</i>) Ruiz & Pavon	38, 59, 76

Table 2. (Continued) Reported hosts and nonhosts for *Rotylenchulus reniformis* according to numeric literature references as footnoted.

	<i>Lepidium virginicum</i> L.	92		<i>Nerium oleander</i> L.	5, 54
	<i>Leucas urticaefolia</i> R. Br.	51		<i>Nicotiana tabacum</i> L.	7, 57, 68, 73, 74
	<i>Litchi chinensis</i> Sonn.	46		<i>Nolina</i> (= <i>Beaucarnea</i>) <i>recurvata</i> (Lem.) Hemsl.	90
	<i>Luffa acutangula</i> (L.) Roxb.	46		<i>Olea europaea</i> L.	3
	<i>Luffa cylindrica</i> (L.) M. Roem.	44	H/NH	<i>Oryza sativa</i> L.	12, 46
H/NH	<i>Lycopersicon esculentum</i> Mill.	10, 47, 56, 73, 74, 77, 87		<i>Parietaria floridana</i> Nutt.	Pers. comm., R. N. Insetra
H/NH	<i>Lycopersicon pimpinellifolium</i> (Juss.) Mill.	10, 77		<i>Parthenium crispum</i> (Mill.) Airy-Shaw	92
	<i>Macropitium</i> (= <i>Phaseobus</i>) <i>lathyroides</i> (L.) Urban	56		<i>Parthenium hysterophorus</i> L.	38, 59, 65, 76
	<i>Malpighia glabra</i> L.	25		<i>Paspalum conjugatum</i> Berg.	86
	<i>Mahoeviscus arboreus</i> Cav.	104	NH	<i>Paspalum dilatatum</i> Poir.	12
	<i>Mangifera indica</i> L.	9, 66, 100		<i>Paspalum fasciculatum</i> Willd. ex Fluegge	86
	<i>Manihot esculenta</i> Crantz	6, 73, 74		<i>Passiflora edulis</i> Sims.	48
	<i>Mentha</i> sp.	22		<i>Passiflora seemanni</i> Griseb.	56
	<i>Merremia</i> (= <i>Ipomea</i>) <i>tuberosa</i> (L.) Rendle	56		<i>Persea americana</i> (= <i>gratissima</i>) Mill.	57, 74
H/NH	<i>Mimosa pudica</i> L.	6, 76		<i>Phaseobus lunatus</i> (= <i>limensis</i>) L.	12, 56
	<i>Modiola caroliniana</i> (= <i>multida</i>) (L.) G. Don	13, 104		<i>Phaseobus semierectus</i> L.	57
NH	<i>Mollugo hirta</i> (author uncertain)	51		<i>Phaseobus vulgaris</i> L.	1, 12, 44, 56, 63, 73, 74
	<i>Momordica balsamina</i> L.	92		<i>Phenax sonneratii</i> Wedd.	76
	<i>Momordica charantia</i> L.	44		<i>Philodendron bipinnatifidum</i> (= <i>selloum</i>) Endl.	90
NH	<i>Mucuna</i> (= <i>Stylobolium</i>) <i>pruriens</i> (= <i>derringtona</i>) (L.) DC. var. <i>utilis</i> (Wallich ex Wight) Baker ex Burck	74	NH	<i>Phlox drummondii</i> Hook.	56
	<i>Murraya paniculata</i> (= <i>exotica</i>) (L.) Jack	56		<i>Phoenix roebelenii</i> O'Brien	41
	<i>Musa acuminata</i> Colla	75		<i>Phyllanthus amarus</i> Schumacher	76
	<i>Musa martinii</i> Hort. ex Carriere	92	NH	<i>Phyllanthus carolinensis</i> Walter	38, 65
	<i>Musa paradisiaca</i> L.	6		<i>Phyllanthus niruri</i> L.	51
NH	<i>Myristica fragrans</i> Houtt.	50		<i>Phyllanthus urinaria</i> L.	76
NH	<i>Neodypsis decaryi</i> Jumelle	41		<i>Physalis angulata</i> L.	76
NH	<i>Neodypsis lastelliana</i> Baill.	41		<i>Pilea microphylla</i> (L.) Liebm.	38
				<i>Piper belle</i> L.	1
				<i>Piper nigrum</i> L.	50

Table 2. (Continued) Reported hosts and nonhosts for *Rotylenchulus reniformis* according to numeric literature references as footnoted.

	<i>Pisum sativum</i> L.	56			<i>Rotylenchulus cochinchinensis</i> (= <i>exaltata</i>) (Lour.) 76,92
	<i>Polyscias guilfoylei</i> (Bull.) L. H. Bailey	56		Clayton	
	<i>Portulaca oleracea</i> L.	38, 56, 76	NH	<i>Sabal palmetto</i> (Walt.) Lodd. ex Schult. & Shult.f.	41
	<i>Prosopis glandulosa</i> (= <i>chilensis</i>) Torr.	56			
	<i>Prunus armeniaca</i> L.	46	H/NH	<i>Saccharum officinarum</i> L.	7, 11, 12, 67
	<i>Prunus institiia</i> (= <i>bokhariensis</i>) Poir.	46		<i>Sansevieria trifasciata</i> Prain.	90
	<i>Prunus persica</i> (L.) Batsch.	46		<i>Schefflera</i> (= <i>Brassaia</i>) <i>actinophylla</i> (Endl.) Harms	90
	<i>Psophocarpus tetragonolobus</i> (L.) DC.	4			
NH	<i>Psychotherma elegans</i> (R.Br.) Blume	41		<i>Schefflera</i> (= <i>Brassaia</i>) <i>arboricola</i> (Hayata) Merr.	90
	<i>Pueraria montana</i> (= <i>hirsuta</i> = <i>thumbergiana</i>) (Lour.) mer. var. <i>lobata</i> (Willd.)	57, 93		<i>Schinus terebinthifolius</i> Raddi	56, 91
	<i>Pueraria phaseoloides</i> (Roxb.) Benth.	92		<i>Senna</i> (= <i>Cassia</i>) <i>torta</i> (L.) Roxb.	19
	<i>Pyrus malus</i> L.	46		<i>Sesamum indicum</i> L.	92
NH	<i>Quercus calliprinos</i> Webb	22		<i>Sesbania exaltata</i> (raf.) V.L. Cory	14
	<i>Radermachera sinica</i> (Hance) Hemsl.	90		<i>Setaria barbata</i> (Lam.) Kunth	76
	<i>Raphanus sativus</i> L.	56		<i>Setaria glauca</i> (L.) Beauv. [= <i>Pennisetum typhoides</i> (Burm.) Stapf & C. E. Hubb]	45
NH	<i>Ravenea rivularis</i> Jumelle & Perrier	41			
NH	<i>Rhapis excelsa</i> L.f.	41	H/NH	<i>Sida rhombifolia</i> L.	92, 104
	<i>Rhynchosia aurea</i> DC.	84		<i>Sida spinosa</i> L.	14
	<i>Rhynchosia bracteata</i> Benth. ex Baker	84		<i>Solanum melongena</i> L.	47, 56, 73, 74
	<i>Rhynchosia cana</i> DC.	84		<i>Solanum nigrum</i> L.	56
	<i>Rhynchosia densiflora</i> (Roth) DC.	84		<i>Solanum tuberosum</i> L.	56
	<i>Rhynchosia minima</i> (L.) DC.	84		<i>Solenostemon</i> (= <i>Coleus</i>) <i>scutellaroides</i> (L.) Codd.	56
	<i>Rhynchosia rothii</i> (author uncertain)	84		<i>Sonchus oleraceus</i> L.	65
	<i>Rhynchosia rufescens</i> DC.	84	H/NH	<i>Sorghum bicolor</i> (= <i>Andropogon sorghum</i>) (L.) Moench	6, 12, 56, 65
	<i>Rhynchosia suaveolens</i> DC.	84			
	<i>Rhynchosia sublobata</i> (Schum.) Meikle	84		<i>Sorghum halepense</i> (L.) Pers.	14
	<i>Richardia scabra</i> L.	56	NH	<i>Spermaceae assurgens</i> Ruiz & Pavon	76
	<i>Ricinus communis</i> L.	10, 30, 44, 47, 92	NH	<i>Spermaceae confusa</i> Rendle	76

Table 2. (Continued) Reported hosts and nonhosts for *Rotylenchulus reniformis* according to numeric literature references as footnoted.

NH	<i>Spermacoce latifolia</i> Pohl ex DC.	76	<i>Urena lobata</i> L.	104
H/NH	<i>Spinacia oleracea</i> L.	12, 44, 47	<i>Vernonia cinerea</i> (L.) Less.	56, 76, 92
	<i>Stachys arvensis</i> L.	56	<i>Vicia faba</i> L.	98
NH	<i>Stachytarpheta jamaicensis</i> (L.) Vahl	76	<i>Vicia villosa</i> Roth	12, 57
NH	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	41	<i>Vigna acanitifolia</i> (Jacq.) Marechal	69, 73, 74
	<i>Synedrella nodiflora</i> (L.) Gaertner	73	<i>Vigna radiata</i> (L.) R. Wilczek (= <i>Phaseolus aureus</i> Roxb.)	1, 17
	<i>Syzygium</i> (= <i>Eugenia</i>) <i>malaccense</i> (L.) Merr. & L. M. Perry	56	<i>Vigna unguiculata</i> (L.) Walp.	8, 29, 34, 40, 41, 42, 43, 47, 56, 73, 94
	<i>Tagetes erecta</i> L.	12, 56		
	<i>Tagetes patula</i> L.	18, 56	<i>Vigna mungo</i> (L.) Hepper	1, 46
	<i>Theobroma cacao</i> L.	50	<i>Vitis vinifera</i> L.	95
NH	<i>Thrinax morrisii</i> H. Wendl	41	<i>Waltheria indica</i> L.	38
	<i>Trachycarpus fortunei</i> (Hook.) H. Wendl.	39, 41	<i>Washingtonia robusta</i> H. Wendl.	41
NH	<i>Trianthema portulacastrum</i> L.	51	<i>Wodyetia bifurcata</i> A. K. Irvine	39, 41
	<i>Tribulus terrestris</i> L.	51	<i>Xanthium</i> sp.	19
	<i>Trichosanthes dioica</i> Roxb.	71	<i>Xanthosoma caracu</i> Koch & Bouche'	64
	<i>Trifolium alexandrinum</i> L.	62	<i>Xanthosoma nigrum</i> (= <i>violaceum</i>) [(Vell.) Conc.] Mansf.	64
	<i>Trifolium incarnatum</i> L.	12	<i>Xanthosoma sagittifolium</i> (= <i>atrovirens</i>) (L.) Schott	64, 92
	<i>Trifolium pratense</i> L.	12		
	<i>Trifolium repens</i> L.	12	<i>Youngia</i> (= <i>Crepis</i>) <i>japonica</i> (L.) DC.	38, 56
	<i>Trigonella foenum-graecum</i> L.	46	<i>Zea mays</i> L.	12, 36, 56, 65, 87, 103
	<i>Triticum aestivum</i> L.	47	<i>Zinnia elegans</i> Jacq.	56

examined (Table 2). Host classifications were largely consistent, and we found conflicting host reports for only 22 species (6% of all plant species examined). However, in the few cases where they occur, contradictory or incorrect host status assignments can be very important from a regulatory or crop rotation standpoint. This is particularly true for container-grown citrus trees (*Citrus* spp.) and ornamentals produced for export.

Gaur and Perry (1991b) noted that *R. reniformis* "preferred" dicotyledons. This may prove correct once enough plant species have been examined. About 76% of the 210,000 known species of angiosperms are dicots (Correll and Johnston, 1979) and almost the same percentage (78%) of the 364 plant species that have been examined as potential hosts for *R. reniformis* were dicots. In contrast, the overall incidence of nonhosts among monocots examined (33%) was much higher than among dicots (9%) as predicted by Gaur and Perry; however, most (18 of 26) of the monocot nonhosts that are known are palms (family Arecaceae/Palmae) and at present the incidence of known hosts for *R. reniformis* among other monocots (86%) is nearly as high as that reported for dicots (91%).

We found 77 plant families to contain reported hosts of *R. reniformis*. Many of these are tropical families in which only one or two species have been tested. The plant families which have received the most intense investigation as hosts of *R. reniformis* are Araceae, Arecaceae/Palmae, Asteraceae/Compositae, Euphorbiaceae, Fabaceae/Leguminosae, Malvaceae, Poaceae/Graminae, and Solanaceae. All contain crop or ornamental species of major economic importance. Araceae, Arecaceae/Palmae, and Poaceae/Graminae are monocot families; the others are dicots.

Immune and resistant plants: We found only 74 plant species to have been reported to be nonhosts and 22 of these have also been classified as hosts by some investigators (Table 3). Subspecific differences between the plants tested by different investigators undoubtedly have caused some differences in host status assignment. For example, turnip (*Brassica rapa*) was considered a nonhost by Birchfield and Brister (1962) whereas Chinese cabbage (*Brassica rapa* var. *pekinensis*) was classified as a host by Linford and Yap (1940). In some susceptible crops, certain cultivars or breeding lines are immune or highly resistant; a few breeding lines of tomato (*L. esculentum*) and accessions of *L. pimpinellifolium*, for example, are immune (Balasubramanian and Ramakrishnan, 1983; Rebois *et al.*, 1973). In some crop species, most cultivars are so highly resistant that populations almost invariably decrease in rotation studies and females with eggs can be found only with great difficulty or under special environmental circumstances. This situation could explain conflicting reports for onion (*Allium cepa*) (Birchfield and Brister, 1962; Carter, 1981a; Khan, 1985; Singh, 1975), bermudagrass (*Cynodon dactylon*) (Birchfield and Brister 1962; Lal *et al.*, 1976; Singh, 1975), rice (*Oryza sativa*) (Birchfield and Brister, 1962; Khan, 1975), pepper (*C. annuum*) (Birchfield and Brister, 1962; Routaray *et al.*, 1988; Sivakumar *et al.*, 1979), and some species of *Crotalaria* (Birchfield and Brister, 1962; Caswell *et al.*, 1991; Peacock, 1956b; Soares da Silva *et al.*, 1989). A histological study of onion showed that infrequent but normal trophic site development and nematode reproduction did occur on six cultivars when inoculated separately with three isolates of *R. reniformis* (Carter, 1981a). In one pot study on *Z. mays* (Windham and Lawrence, 1992), the resistance in 50 com-

Table 3. Contradictory host reports for *Rotylenchulus reniformis*.

Plant species	Host records	Nonhost records
<i>Allium cepa</i> L.	Singh, 1975; Carter, 1981a	Birchfield and Brister, 1962; Khan, 1985; Khan and Khan, 1973
<i>Allium sativum</i> L.	Stoyanov, 1967	Khan and Khan, 1973
<i>Brassica nigra</i> (L.) W. D. J. Koch	Khan and Khan, 1969	Birchfield and Brister, 1962
<i>Brassica rapa</i> L.	Linford and Yap, 1940	Birchfield and Brister, 1962; Khan, 1985
<i>Canavalia ensiformis</i> (L.) DC.	Stoyanov, 1967	Peacock, 1956b
<i>Capsicum annuum</i> L.	Routary <i>et al.</i> , 1988	Birchfield and Brister, 1962; Sivakumar <i>et al.</i> , 1979
<i>Citrus limon</i> (L.) Burm. f.	Peacock, 1956a, 1956b	Inserra and Duncan, 1996
<i>Coffea canephora</i> (= <i>robusta</i>) Pierre & Froehner	Valdez, 1968a	Macedo, 1974; Peacock, 1956b
<i>Crotalaria juncea</i> L.	Caswell <i>et al.</i> , 1991; Peacock, 1956b	Soares da Silva <i>et al.</i> , 1989
<i>Crotalaria pallida</i> Desv.	Peacock, 1956b	Soares da Silva <i>et al.</i> , 1989
<i>Crotalaria spectabilis</i> Roth	Linford and Yap, 1940	Soares da Silva <i>et al.</i> , 1989
<i>Cynodon dactylon</i> (L.) Pers.	Singh, 1975	Birchfield and Brister, 1962; Lal <i>et al.</i> , 1976
<i>Cyperus rotundus</i> L.	Singh, 1974	Lal <i>et al.</i> , 1976
<i>Daucus carota</i> L.	Peacock, 1956a; Linford and Yap, 1940	Khan and Khan, 1973
<i>Echinochloa crus-galli</i> (L.) Beauvois	Carter <i>et al.</i> , 1995	Birchfield and Brister, 1962
<i>Oryza sativa</i> L.	Khan, 1975	Birchfield and Brister, 1962
<i>Saccharum officinarum</i> L.	Mehta and Sundara, 1989	Ayala, 1962; Birchfield and Brister, 1962; Birchfield, 1972
<i>Sida rhombifolia</i> L.	Stoyanov, 1967	Yik and Birchfield, 1984
<i>Sorghum bicolor</i> (= <i>vulgare</i>) (L.) Moench	Peacock, 1956b	Birchfield and Brister, 1962
<i>Spinacea oleracea</i> L.	Khan and Khan, 1969	Birchfield and Brister, 1962

mercial hybrids was so high that populations remained below inoculum levels in all cases, with final populations for 46 hybrids less than 1% of the control [*cotton* (*G. hirsutum*) cv. Delta and Pineland 20]. Although no eggs whatsoever were found on 15 of the hybrids, the term "immune" was avoided and these plants were considered to be highly resistant.

An unsuspected potential cause of host status misassignment was discovered by Inserra and Duncan (1996) in pots containing both rough lemon (*Citrus limon*) and cowpea (*V. unguiculata*) plants; cowpea roots that supported normal nematode reproduction were entangled and easily confused with citrus roots, which supported no reproduction. Egg masses

produced by females on cowpea roots were sometimes found adhering to rough lemon roots. In ornamental palm plantings and in citrus groves where weeds or cover crops occur, soil samples can easily contain roots from more than one plant species and in many cases, examinations of roots extracted from such samples could have led to host misidentification. Most common weeds are good hosts (Carter *et al.*, 1995; Edmunds, 1971; Gnanapragasam *et al.*, 1989; Inserra *et al.*, 1989; Quénehervé *et al.*, 1995). The lack of reproduction of *R. reniformis* on citrus was confirmed by a host test conducted in Brazil using the citrus rootstock Rangpur lime (*Citrus limonia*), which was immune to nematode infection (Goulart and Monteiro, 1995).

Recent studies in Florida have clarified some ambiguities regarding the host status of ornamental palms (Arecaceae/Palmae). Of 20 palms tested by Inserra *et al.* (1991, 1994), only two were found to support any reproduction and in both cases (*Washingtonia robusta* and *Acoelorrhaphe wrightii*) final populations were only a fraction of the initial inoculum level. Previous associations of *R. reniformis* with certain palm species likely resulted from reproduction on weed hosts. Avocado (*Persea americana*) and mango (*Mangifera indica*) are listed as hosts for *R. reniformis* in the literature (Table 2); however, in a host test conducted in Florida, there was no evidence of nematode reproduction on the roots of these plants maintained for one year in soil infested with a nematode population from south Florida (Inserra, unpublished).

Host races of *R. reniformis* may account for some of the differences in host status observed by different investigators. Occurrence of a race incapable of reproducing on castor (*R. communis*) or Upland cotton in India, for example, is well established (Dasgupta and Seshadri, 1971a, 1971b).

Other populations in India reproduce on castor and cotton. Differences in reproduction and damage caused by 17 populations from the United States on certain cultivars of cotton and soybean also have been observed (McGawley and Overstreet, 1995; pers. comm., E. C. McGawley, Louisiana State University). Sugarcane was originally considered immune to populations in Hawaii (Linford and Yap, 1940) and Louisiana (Birchfield and Brister, 1962), and reports of associations of high population densities of *R. reniformis* with sugarcane in Puerto Rico and the Dominican Republic led to speculation regarding occurrence of host races (Birchfield and Brister, 1962). Subsequent rigorous examinations for reproduction on sugarcane by Puerto Rican populations, however, revealed no reproduction (Ayala, 1962; Roman, 1964). Nonetheless, a population from India has been shown to reproduce on sugarcane under controlled conditions (Mehta and Sundara, 1989). The physiological differences required for a population of *R. reniformis* to reproduce on sugarcane may be simple, since sugarcane is a good host for *R. parvus* (Van den Berg and Spaull, 1981). There is additional evidence of differences between certain Indian populations and those from other parts of India and the world. Some cultivars of *Z. mays* (Srivastava and Sethi, 1986) and *C. annuum* (Routaray *et al.*, 1988), for example, are apparently good hosts for some Indian populations of *R. reniformis*. These plant species are considered highly resistant or immune to other populations of *R. reniformis*.

In Japan, three morphologically and reproductively different types of populations of *R. reniformis* occur, which are referred to as male numerous type (MNT), male rare type (MRT) and male absent type (MAT) (Nakasono, 1983). The MRT and MAT populations reproduce parthe-

nogenetically; MNT populations reproduce amphimictically. In addition, MRT and MAT populations occur at more northern, cooler latitudes and have narrower host ranges than MNT populations. It is noteworthy that in Cuba, an amphimictic population of *R. reniformis* has been shown to be capable of producing viable but noninfective progeny parthenogenetically (Rodríguez-Fuentes and Añorga-Morales, 1977).

It is never possible to say with absolute certainty that a given plant genotype is a nonhost. On some genotypes, nematode reproduction may be so low that numerous root systems must be examined carefully before a single gravid female is found. From a practical standpoint, therefore, the appropriate criteria for distinguishing between hosts and non-hosts depends somewhat on the intended application. For regulatory purposes, any egg production at all can cause contamination problems in nurseries certified for this pest (Inserra *et al.*, 1991, 1994b). In contrast, a low level of reproduction would be unimportant in a resistant rotational crop if recontamination of the field by wind, water, and nematode reproduction on weed hosts were impossible to avoid.

Economic impact. Many studies have been done to estimate the impact of *R. reniformis* on crops around the world. As with other nematodes, the approaches taken have been to measure plant growth responses to a graded series of inoculum levels in pots or microplots, or measure yield responses to nematicide or crop rotation treatments. Each approach of course has its limitations. Damage levels measured in pots can differ substantially from those under field conditions, while in field plantings, many factors other than the nematode can contribute to the responses observed. As noted by Gaur and Perry (1991b), pot studies with graded inoculum levels of *R. reniformis* indicate

that damage to a wide array of plants can occur at densities between 0.1 and 5 nematodes/cm³ of soil (Acharya and Padhi, 1987; Acosta and Ayala, 1975; Ahmad, 1989; Ferraz and Sharma, 1979; Gapasin and Valdez, 1979; Gupta and Yadav, 1980; Khan and Husain, 1989b, 1990; Mishra and Gaur, 1981; Padhi and Misra, 1987; Panda and Seshadri, 1979; Rebois *et al.*, 1978; Sahoo and Padhi, 1986; Sud *et al.*, 1984; Varaprasad *et al.*, 1987).

Rotylenchulus reniformis is considered a serious problem in Upland cotton throughout the southeastern United States (Heald and Robinson, 1990) (Fig. 12) and population thresholds for nematicide application have been developed based on results of numerous field trials (Beltwide Cotton Nematode Survey, 1994; Lawrence and McLean, 1996). The agricultural university extension services in Mississippi and Alabama recommend treatment if the *R. reniformis* population density exceeds 2 nematodes/cm³ in the spring or 10 nematodes/cm³ in the fall or winter (Blasingame and Patel, 1987). Corresponding thresholds in Louisiana are 1 and 5 nematodes/cm³ soil (pers. comm., C. Overstreet, Louisiana State University). Population densities exceeding all of these thresholds are commonly encountered in the Mississippi Delta production region (Lawrence and McLean, 1996), the Red River Basin (Overstreet and McGawley, 1996), and the Lower Rio Grande Valley (Robinson *et al.*, 1987). These densities are much higher than are typically encountered for *Meloidogyne* species in cotton fields (Starr *et al.*, 1993). *Rotylenchulus reniformis* does not occur in Arizona, California, and New Mexico (Heald and Robinson, 1990).

In plot experiments conducted in south Florida, positive yield response on snap bean (*Phaseolus vulgaris*) was obtained with non-fumigant nematicide (oxamyl)



Fig. 12. Stunted plants in a cotton field infested by *Rotylenchulus reniformis* in Alabama. (Courtesy of W. S. Gazaway).

treatment at population levels of 4 or more *R. reniformis*/cm³ soil. With lower populations, use of the nematicide was not consistent in increasing snap bean yield (McSorley *et al.*, 1981b). Results of other plot experiments conducted in south Florida showed an inverse relationship between snap bean yield and the number of *R. reniformis* in the soil (McSorley, 1980). However, at the greatest population densities (9 *R. reniformis*/cm³ of soil) the yield suppression did not exceed 25% (Fig. 13). At the population levels that usually occur in Florida soils (4-5 nematodes/cm³ of soil), nematode damage on snap bean averages *ca.* 10% (Fig. 13) (McSorley, 1980). These results indicate that *R. reniformis* at high population densities on snap bean in Florida has less destructive effect than root-knot nematodes (*Meloidogyne*

spp.). However, crop loss of greater magnitude is routinely reported for cotton growing in fields infested with *R. reniformis* in Louisiana (206,000 ha) and Mississippi (283,000 ha). Losses in these two states have been assessed as high as 40-60%, but average 15-30% (Overstreet, 1996).

On various legume and vegetable crops, particularly in India, nematicide treatment is not cost effective, and management through use of resistant and tolerant cultivars or with cultural methods, such as crop rotation, fallow, weed control, *etc.*, is preferable. In field crops, appreciable effort has been put toward the identification of resistant germplasm and the development of resistant cultivars.

Regulatory considerations: In addition to being a damaging pest of field and vegetable crops, *R. reniformis* is of economic



Fig. 12. Stunted plants in a cotton field infested by *Rotylenchulus reniformis* in Alabama. (Courtesy of W. S. Gazaway).

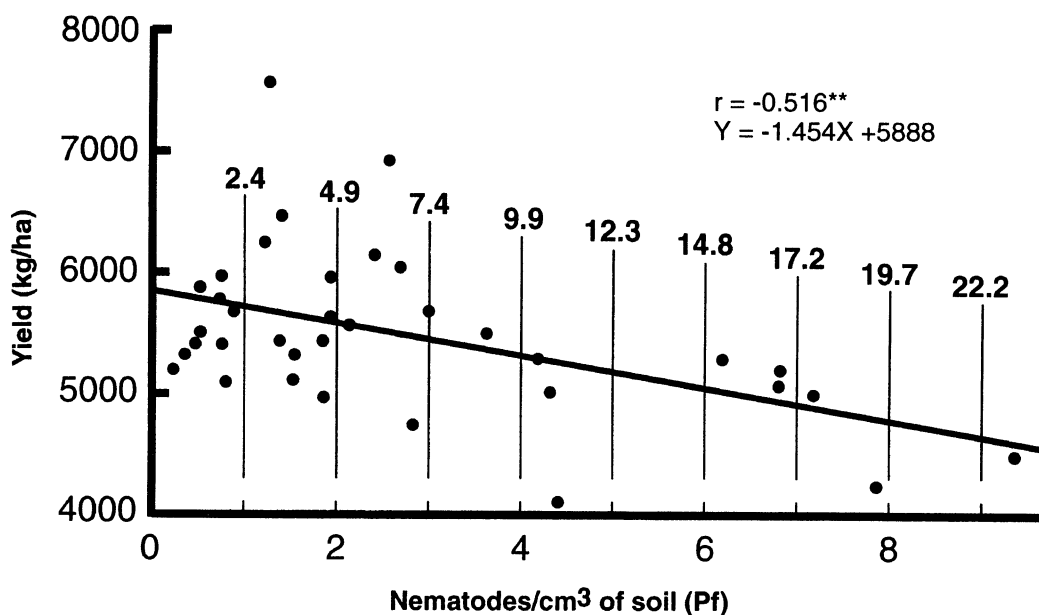


Fig. 13. Relationship of snap bean yield to final population (Pf) of *Rotylenchulus reniformis* in treated and untreated plots. Values on top of each vertical bar indicate percentage of yield loss observed at each *R. reniformis* population level compared to the chemically disinfested plots. The regression equation is based on numbers of nematodes per 100 cm³ soil. (After McSorley, 1980).

importance to ornamental industries established in areas where the nematode is present because of the quarantine restrictions imposed by some states to plant shipments contaminated by this parasite. In the United States, the states of Arizona, California, and New Mexico enforce quarantines against the reniform nematode in order to protect their cotton industries from this pest. Chile and Switzerland list *R. reniformis* among the noxious organisms subject to quarantines.

Crop resistance: Resistant breeding lines and cultivars were tabulated by Varaprasad (1986) and updated by Gaur and Perry (1991b). We have combined this information with that gathered from other sources, omitted most species for which germplasm screening studies *per se* were not found, and deleted names of resistant cultivars or breeding lines, to conserve space (Table 4). Based on the number of

genotypes examined and the number of papers published, most work has been done on Upland cotton and soybean in the United States, and on various staple legumes in India and Pakistan. The availability of sources of resistance to *R. reniformis* in these crops varies greatly. Certain cultivars of tomato and soybean, for example, have very high levels of resistance. In cowpea, a few acceptably resistant cultivars have been identified. In Upland cotton, no cultivars with high levels of resistance are available. However, several high-yielding breeding lines have been developed that are tolerant to *R. reniformis* and are adapted to the Lower Rio Grande Valley (Cook *et al.*, 1997). Four additional lines developed under Louisiana conditions have a low level of resistance and have been released for commercial development (Jones *et al.*, 1988). Incorporating resistance from related *Gossypium* species

Table 4. Studies identifying crop germplasm with resistance to *Rotylenchulus reniformis*.

Blackgram, urdbean (<i>Vigna mungo</i> L.) Routaray <i>et al.</i> , 1986	Papaya (<i>Carica papaya</i> L.) Patel <i>et al.</i> , 1989b
Castor (<i>Ricinus communis</i> L.) Darekar <i>et al.</i> , 1990	Pepper and related plants (<i>Capsicum</i> spp.) Birchfield and Brister, 1962
Chickpea (<i>Cicer arietinum</i> L.) Anver and Alam, 1990, 1995 Sahoo <i>et al.</i> , 1986	Peacock, 1956a Routaray <i>et al.</i> , 1988
Coffee (<i>Coffea</i> spp.) Macedo, 1974 Peacock, 1956a Schenck and Schenck, 1994	Pigeonpea [<i>Cajanus cajan</i> (L.) Mill] Chavda <i>et al.</i> , 1988 Patel <i>et al.</i> , 1987 Thakar and Yadav, 1985, 1986, 1987
Cotton and related plants (<i>Gossypium</i> spp.) Beasley, 1986 Birchfield and Brister, 1963 Blasingame, 1991 Cook <i>et al.</i> , 1997 Cook <i>et al.</i> , 1996 Jones <i>et al.</i> , 1988 Khadr <i>et al.</i> , 1972 Minton, 1964 Muhammad and Jones, 1990 Muralidaran and Sivakumar, 1977 Neal, 1954 Shepherd, 1983 Yik and Birchfield, 1984	Potato (<i>Solanum tuberosum</i> L.) Montasser <i>et al.</i> , 1992 Rebois and Webb, 1979
Cowpea (<i>Vigna unguiculata</i> L.) Gaur, 1986 Haque, 1992 Haque and Padmavathy, 1986 Khan and Husain 1988, 1989b Makadia <i>et al.</i> , 1987 Thakar and Patel, 1985	Soybean (<i>Glycine max</i> (L.) Merr.) Anand, 1992 Birchfield and Brister, 1969 Birchfield and Williams, 1974 Birchfield <i>et al.</i> , 1971 Cornelius and Lawrence, 1993 Good, 1972 Hartwig and Epps, 1973, 1977 Hartwig <i>et al.</i> , 1988 Harville <i>et al.</i> , 1988 Lim and Castillo, 1979 Rebois <i>et al.</i> , 1968, 1970 Robbins <i>et al.</i> , 1994a, 1994b Williams <i>et al.</i> , 1981
Horsegram (<i>Dolichos uniflorus</i> Lam.) Nayak <i>et al.</i> , 1987	Sweet potato [<i>Ipomoea batatas</i> (L.) Lam.] Clark and Wright, 1983 Good, 1972 Martin <i>et al.</i> , 1966
Greengram, mungbean (<i>Phaseolus aureus</i> Roxb. = <i>Vigna radiata</i> (L.) R. Wilczek) Patel <i>et al.</i> , 1989a	Tobacco (<i>Nicotiana tabacum</i> L.) Heald and Meredith, 1987 Patel, 1986
	Tomato and related plants (<i>Lycopersicon</i> spp.) Balasubramanian and Ramakrishnan, 1983 Germani, 1978b

Table 4. (Continued) Studies identifying crop germplasm with resistance to *Rotylenchulus reniformis*.

Patel and Thakar, 1986	Montasser, 1986
Routaray <i>et al.</i> , 1986	Rebois <i>et al.</i> , 1973
Olive (<i>Olea europaea</i> L.)	Subramanian <i>et al.</i> , 1993
Al-Sayed and Abdel-Hameed, 1991	

(Yik and Birchfield, 1984) is confounded by ploidy and chromosome incompatibilities (Richmond, 1968). As discussed in the previous section on immune plants, there are additional crop species with very high levels of resistance or with immunity, including mustard (*Brassica nigra*), oats, Rhodesgrass (*Chloris gayana*), onion, sugarcane, sunn hemp (*Crotalaria juncea*) and winter wheat (*Triticum aestivum*) (Table 2).

In most cases studied, resistance to *R. reniformis* appears to be inherited, at least in part, independently from resistance to other sedentary nematodes. In Upland cotton, several commercial cultivars and various breeding lines have moderate to high levels of resistance to *Meloidogyne incognita* (Kofoid and White) Chitwood race 3. These have one or both of two relatively strong sources of resistance in their genetic backgrounds: cv. Clewewilt 6 and USDA Cotton Germplasm Collection No. SA 2516 (a wild *G. hirsutum* accession collected in 1947 in Mexico). All *M. incognita*-resistant cultivars of Upland cotton support prolific reproduction by *R. reniformis*. Levels of reproduction by *R. reniformis* vary sufficiently that some breeding lines are considered to have partial resistance; however, inheritance of resistance is complex and new sources of resistance are needed (Muhammad and Jones, 1990). In soybean, high levels of resistance to *R. reniformis* have been found and early studies indicated the same genes conferred resistance to the soybean cyst nematode (*Heterodera glycines* Ichinohe) (Rebois *et al.*,

1968). This prediction, however, has not held up in subsequent genetic studies (Anand, 1992; Birchfield *et al.*, 1971; Gilman *et al.*, 1979; Hartwig and Epps, 1977; Harville *et al.*, 1988). Two pairs of genes with unequal effects are now believed to confer resistance to *R. reniformis* in soybean (Harville, 1985; Williams *et al.*, 1981). In sweetpotato, inheritance of resistance to *R. reniformis* is linked to genes that cause tubers to crack in response to nematode attack and other factors, making tubers unmarketable (Clark and Wright, 1983; Martin, 1960).

Crop rotation and mixed cropping: Management of *R. reniformis* by rotating susceptible crops with nonhost crops has been explored in various regions but apparently has not yet been practiced on a wide scale. The extensive host range of *R. reniformis* severely restricts the options available and further limitations are imposed when other plant-parasitic nematodes or soil-borne pathogens are present. Nonetheless, a number of rotation sequences have been shown to reduce *R. reniformis* populations to nondamaging levels.

Khan *et al.* (1984) in India examined seven 2-year sequences of various combinations of fallow, mung bean (*P. aureus*), carrot (*Daucus carota*), marigold (*Tagetes* sp.), okra (*Abelmoschus esculentus*), wheat, common bean (*P. vulgaris*), Egyptian clover (*T. alexandrinum*), mustard, barley, and sesbania (*Sesbania* sp.), and concluded that mung bean, sesbania, marigold, wheat, barley, and fallow were all effective against

R. reniformis without increasing populations of *Meloidogyne* sp. or *Tylenchorhynchus brassicae* Siddiqi. Haque and Gaur (1985) examined seven other rotations of vegetables in India and found that mung bean, okra, radish (*Raphanus sativus*), chickpea, pea, and maize all resulted in a rapid increase in populations of *R. reniformis* in the soil whereas mustard and sesamum (*Sesamum indicum*) reduced populations. Sivakumar *et al.* (1979) found *R. reniformis* populations to decline faster in pots containing *C. annuum* than in pots containing no plants. Populations of *R. reniformis* also have been shown to decline rapidly in pots containing bermudagrass (Singh, 1975).

Rotylenchulus reniformis has long been a serious problem in the production of pineapple (*Ananas comosus*) in Hawaii. The Hawaiian pineapple industry has now returned to a long planting cycle that includes a fallow period of 6-12 months, providing an opportunity to utilize immune or antagonistic rotational crops (Rohrbach and Apt, 1986). Management of *R. reniformis* by rotating pineapple to sugarcane or pangolagrass (*Digitaria decumbens*) was done in Puerto Rico more than 30 years ago (Roman, 1964). In 1991, Caswell *et al.* examined effects of planting Rhodesgrass, pangolagrass, or sunn hemp in a pineapple field in Hawaii during the intercrop period. Rhoadesgrass reduced populations at least as well as clean fallow 3 months after planting, and populations under sunn hemp 6 months after planting were lower than those in fallow plots. Under greenhouse conditions, population reductions in pots with French marigold (*Tagetes patula*) or with either of two cultivars of Rhodesgrass were greater than in pots without plants. Ko and Schmidt (1993) found that *T. patula* also reduced populations to lower levels than those in fallow plots over a 6-month period in a Hawaiian pineapple field.

In Japan, African marigold (*Tagetes erecta*) and French marigold were compared in rotation with great burdock (*Arctium lappa*), an important vegetable in Japan. *Tagetes patula* was found to have a strong antagonistic effect against *R. reniformis*, while *T. erecta* was a moderately good host (Nakasono, 1973).

Since there are no appreciable levels of resistance to *R. reniformis* in commercial cultivars of Upland cotton, several studies in the United States cotton belt have examined possible rotational crops. Gilman *et al.* (1978) showed that a 1-year rotation of susceptible cotton or susceptible soybean to the resistant soybean cultivar Pickett 71 was extremely effective in reducing the *R. reniformis* population and increasing the yield of the following susceptible crop. However, if the susceptible crop was cotton, high population densities were re-achieved by midseason. A similar, rapid reattainment of high population levels in Upland cotton has been observed also in Israel (pers. comm., D. Orion, The Volcani Center, Bet Dagan). In the United States, maize also has been shown to be an effective rotational crop where it can be economically justified (Lawrence *et al.*, 1991; Rush *et al.*, 1996). Results of rotating maize with crops other than cotton in India have not been particularly encouraging; however, Egunjobi *et al.* (1986) found *R. reniformis* to be only one-ninth as abundant under maize as under cowpea in Nigeria.

A few studies have examined the possibility of intercropping a susceptible crop with antagonistic plants. Yassin and Ismail (1993) planted *Zinnia elegans* in pots containing tomato plants, and Siddiqui and Alam (1987) planted *Tagetes lucida* L. in pots containing tomato, eggplant (*Solanum melongena*), cabbage (*Brassica oleracea* var. *capitata*), or cauliflower. Both *Z. elegans* and *T. lucida* reduced *R. reniformis* populations compared to controls. These plants

may act as trap plants or may directly suppress populations. The nematode-suppressant effects of marigold are well known. Kahn (1985) found that root leachates from five host plant species stimulated hatching, whereas leachates from onion and *Capsicum* spp. suppressed hatch of *R. reniformis* eggs.

**ROTYLENCHULUS SPECIES OF
UNDETERMINED ECONOMIC
IMPORTANCE**

Rotylenchulus borealis

This species has been reported only in Europe and Africa (Fig. 14). In Europe it has been reported from Estonia, France, Germany, Italy, Spain, and The Netherlands (Bello, 1972; Dasgupta *et al.*, 1968; Germershausen and Gunter, 1984; Ryss, 1992). Both females and males have been found. In Africa, *R. borealis* was reported in Benin, Cameroon, Central African Republic, Ghana, Ivory Coast, Kenya, Malawi, Nigeria, and Zimbabwe (Dasgupta *et al.*, 1968; Germani, 1978a; Hillocks *et al.*, 1995). It was erroneously reported from Puerto Rico (Germani, 1978a). The known hosts of this species are all herbaceous plants (Table 5).

Italian populations of *R. borealis* failed to infect Upland cotton cv. Deltapine 16,

peanut (*Arachis hypogaea*) cv. Florunner, pepper cv. Yelowonder, tomato cv. Roma, and durum wheat (*Triticum durum* Desf.) cv. Creso (Vovlas and Inserra, 1982). However, *R. borealis* has been found in cotton and peanut fields in Benin, Cameroon, and Ghana (Germani, 1978a). It also has been found in citrus orchards in Spain (Bello, 1972), in vineyards in Italy (Dasgupta *et al.*, 1968), and in uncultivated land in South Africa (Kleynhans *et al.*, 1996). No host determination, however, was attempted at these sites. The life cycle of *R. borealis* is similar to that of the other reniform nematode species and requires 35-40 days (from egg to egg) at 20-25°C (Vovlas and Inserra, 1982).

Rotylenchulus macrodoratus

This species (Fig. 15) occurs only in the Mediterranean region where it has been reported in France, Greece, Israel, Italy, and Malta (Cohn and Mordechai, 1977; Inserra and Vovlas, 1980; Lamberti and Dandria, 1979; Scotto La Massese, 1973). Both females and males have been found. *Rotylenchulus macrodoratus* is known to parasitize various fruit and ornamental trees and a few herbaceous plants (Table 6).

The life cycle of *R. macrodoratus* (Fig. 16) is similar to that of other reniform

Table 5. Known hosts of *Rotylenchulus borealis*.

Common name	Scientific name
Bean cv. Harvester	<i>Phaseolus vulgaris</i> L.
Corn cv. Dekalb XL-14	<i>Zea mays</i> L.
Green pea cv. Progress	<i>Pisum sativum</i> L.
Potato cv. Alfa	<i>Solanum tuberosum</i> L.
Sorghum cv. N 12	<i>Sorghum bicolor</i> (= <i>vulgare</i>) (L.) Moench
Sweet potato (cv. undetermined)	<i>Ipomoea batatas</i> L.

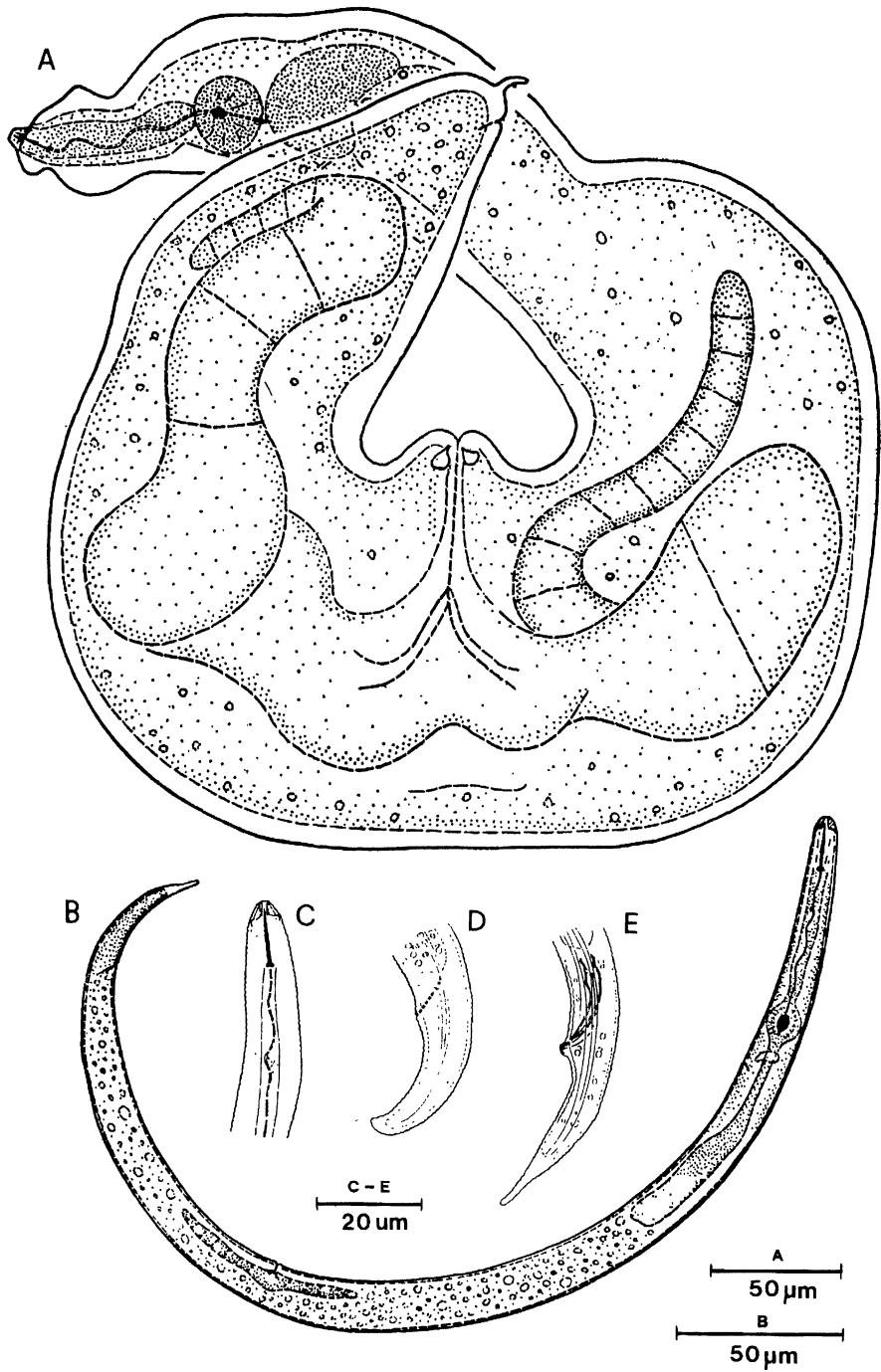


Fig. 14. Life stages of *Rotylenchulus borealis*. A) Mature female. B) Immature female. C) Anterior portion of the body of juvenile. D) Tail of juvenile. E) Tail of male. (After Loof and Oostenbrink, 1962; Dasgupta *et al.*, 1968, modified).

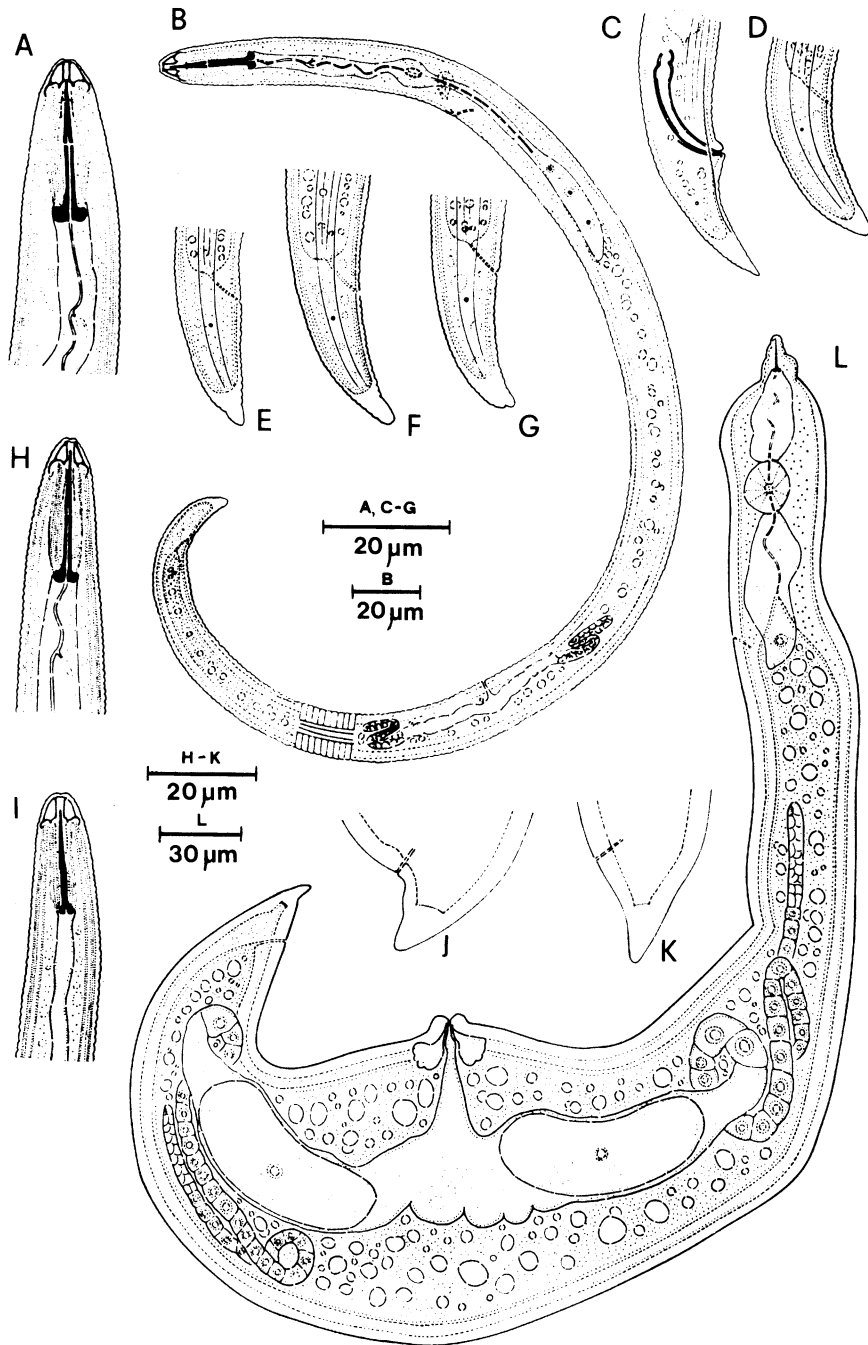


Fig. 15. Life stages of *Rotylenchulus macrodoratus*. A) Anterior portion of the body of immature female. B) Immature female. C) Tail of male. D) Tail of juvenile. E-G) Tail of immature female. H) Anterior portion of the body of juvenile. I) Anterior portion of the body of male. J, K) Tail of mature female. L) Mature female. (After Dasgupta *et al.*, 1968, modified).

Table 6. Known hosts of *Rotylenchulus macrodoratus*.

Common name	Scientific name
Tree hosts	
Almond	<i>Prunus amygdalus</i> L.
Apricot	<i>Prunus armeniaca</i> L.
Carob	<i>Ceratonia siliqua</i> L.
Fig	<i>Ficus carica</i> L.
Grape	<i>Vitis vinifera</i> L.
Laurel	<i>Laurus nobilis</i> L.
Loquat	<i>Eriobotrya japonica</i> Lindl.
Oleander	<i>Nerium oleander</i> L.
Olive	<i>Olea europaea</i> L.
Oak	<i>Quercus calliprinos</i> Webb and <i>Q. farnetto</i> Ten.
Pistacio	<i>Pistacia vera</i> L.
Plum	<i>Prunus domestica</i> L.
Herbaceous hosts	
Carnation	<i>Dianthus caryophyllus</i> L.
Ivy	<i>Hedera ilex</i> L.
Large-flowered sweet William	<i>Dianthus barbatus</i> L.
Pellitory	<i>Parietaria officinalis</i> L.
Phlomis	<i>Phlomis fruticosa</i> L.
Soybean	<i>Glycine max</i> (= <i>hispida</i>) (L.) Merr.

nematode species and requires 45-55 days (from egg to egg) at 18-32°C (Inserra and Vovlas, 1980). As noted previously, the host response induced by *R. macrodoratus* is different from those of other reniform nematodes and involves the formation of a giant uninucleate cell in the root stele (Cohn, 1976; Cohn and Mordechai, 1977; Inserra and Vovlas, 1980; Vovlas and Inserra, 1976). Other reniform nematode species induce the formation of a stelar syncytium in most hosts studied.

Rotylenchulus macrosoma

This species (Fig. 17) has been found in Israel and Syria where it attacks mainly

herbaceous hosts and olive (*Olea europaea*) trees (Table 7) (Cohn and Mordechai, 1988; Sikora and Greco, 1990). Both females and males have been found.

Egyptian, or Sea-island cotton (*Gossypium barbadense*) cv. Acola, pepper (*C. annuum*) cv. Maor, sorghum (*Sorghum bicolor*) cv. D2052, winter wheat (*T. aestivum*) cv. Lakhish, and sour orange (*Citrus aurantium* L.) were non-hosts of *R. macrosoma* (Cohn and Mordechai, 1988). The life cycle of *R. macrosoma* does not differ from that of other *Rotylenchulus* species and includes the induction of a syncytium in host roots (Cohn and Mordechai, 1988).

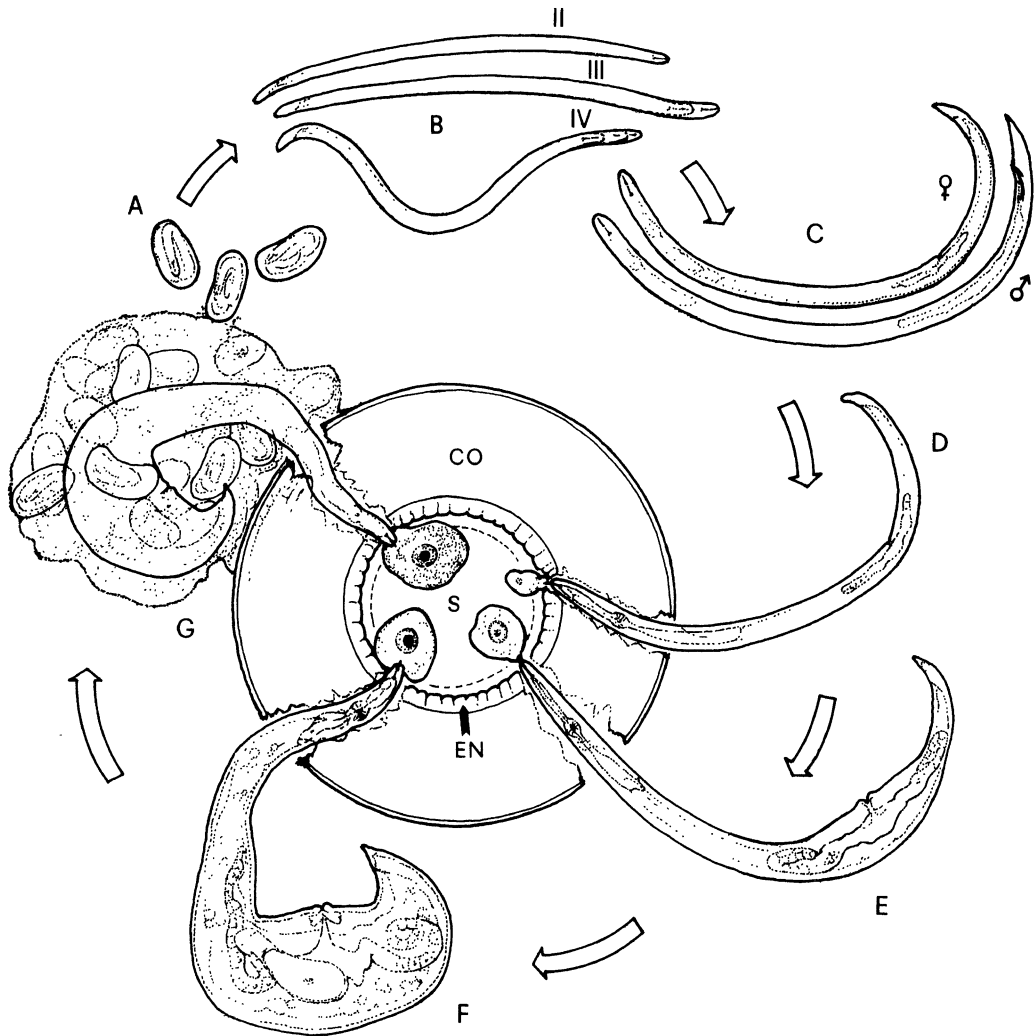


Fig. 16. Life cycle of *Rotylenchulus macrodoratus*. Eggs (A) hatch in the egg mass. Second-stage juveniles (B) emerge from eggs and initiate nematode development in the soil by molting into third-stage juveniles (B), which are followed by fourth-stage juveniles (B), immature females and non-parasitic males (C). Immature females penetrate with the anterior portion of the body into the host root (D), become sedentary, and mate. In the meantime they establish a trophic site in the stele consisting of an uninucleate giant cell, which enlarges during gonad maturation (E,F). They also produce a gelatinous matrix that flows from the vulva and covers the body. Mature females produce eggs, which remain embedded in the gelatinous matrix (G). Gelatinous matrix is not shown in D, E, and F.

Rotylenchulus parvus

This species (Figs. 18, 19) has a wide geographical distribution. It has been reported in North America (Arizona, Cali-

fornia, and Florida) and the Caribbean Basin (St. Croix, St. Thomas, and Dominican Republic) (Dasgupta and Raski, 1968; Garcia-M., 1982; Heyns, 1976; Konicek, 1963; Lehman and Inserra, 1990; Roman

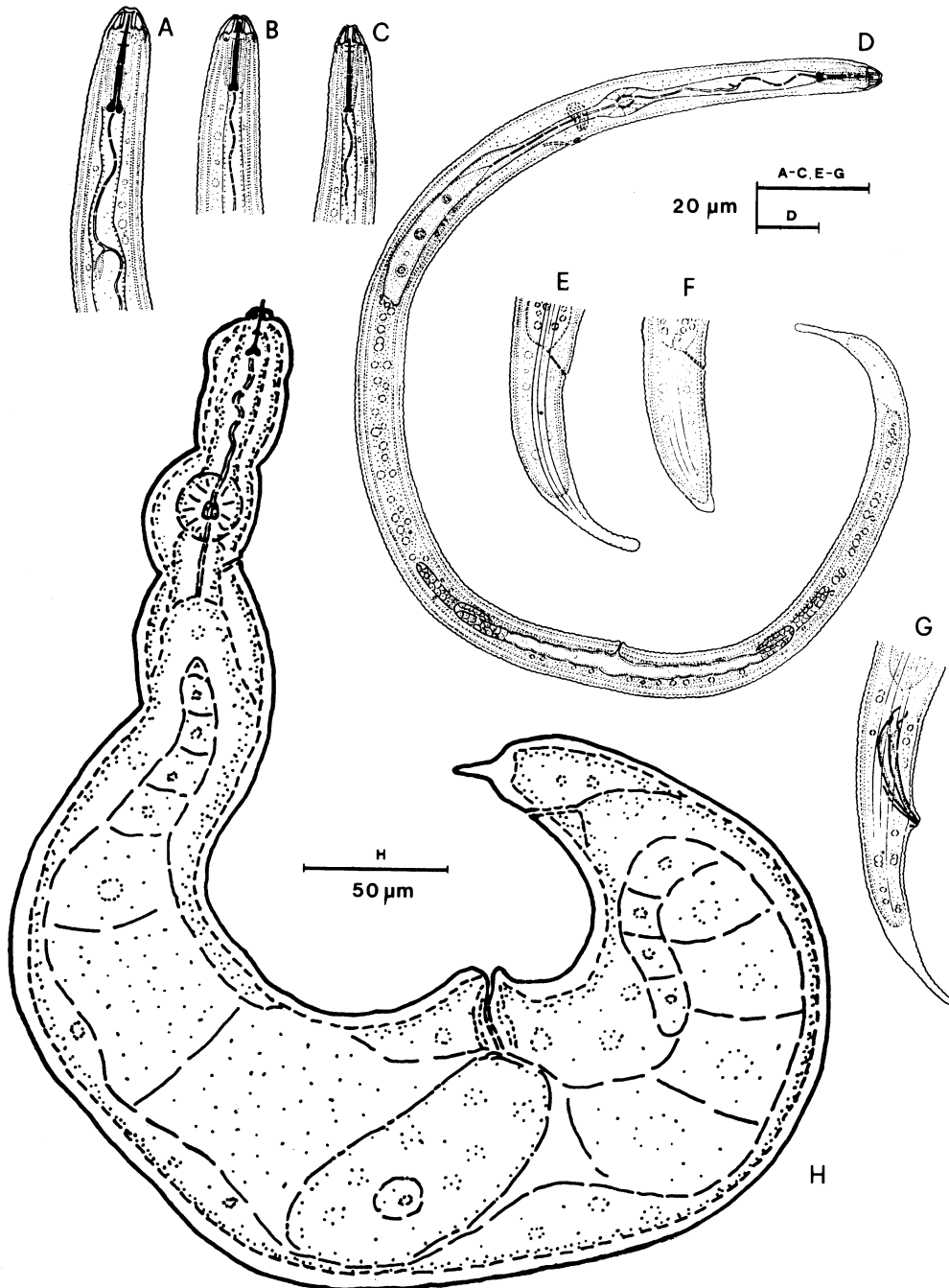


Fig. 17. Life stages of *Rotylenchulus macrosoma*. A) Anterior portion of the body of immature female. B) Anterior portion of the body of juvenile. C) Anterior portion of the body of male. D) Immature female. E) Tail of immature female. F) Tail of juvenile. G) Tail of male. H) Mature female. (After Dasgupta *et al.*, 1968, modified).

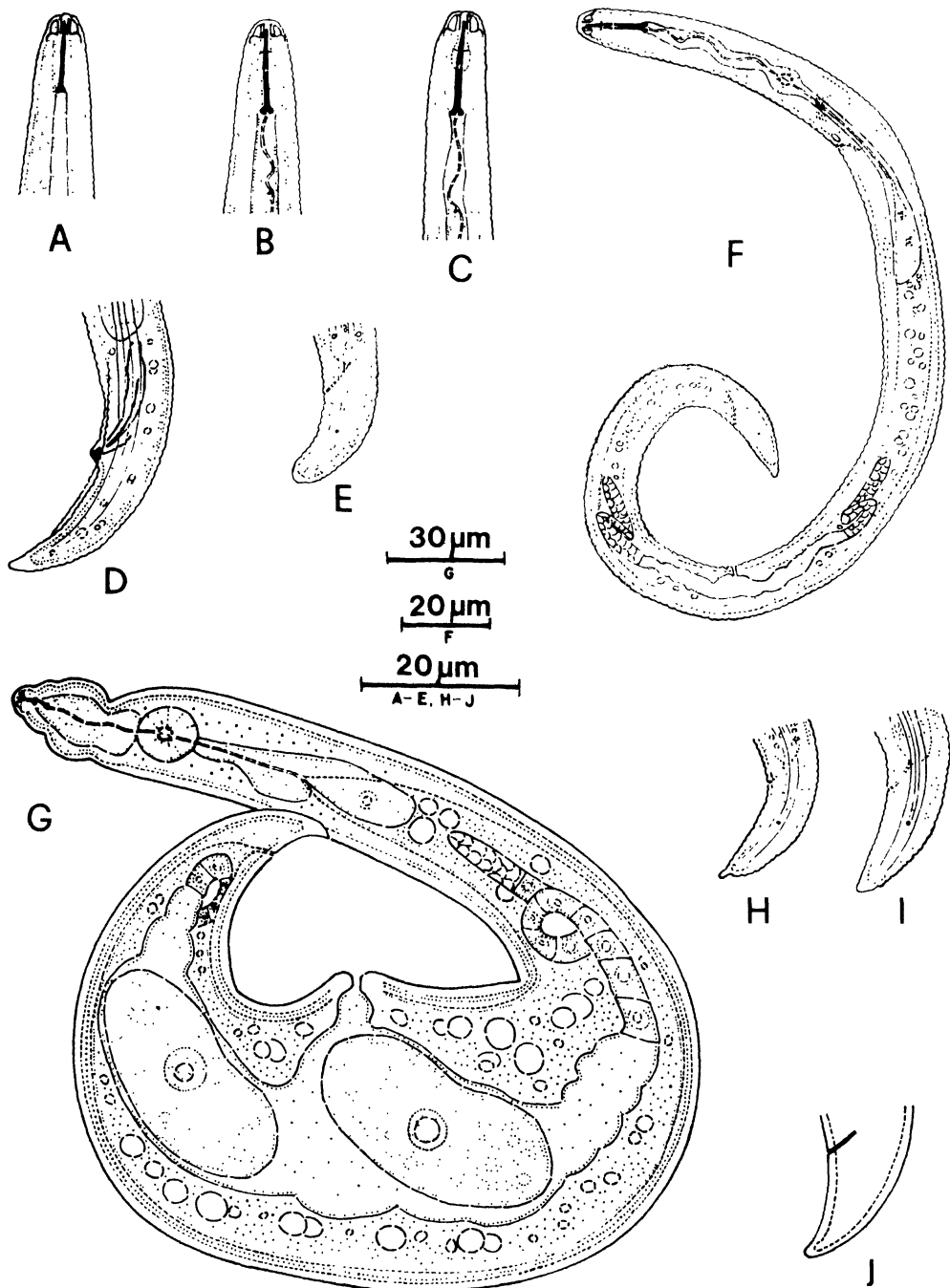


Fig. 18. Life stages of *Rotylenchulus parvus*. A) Anterior portion of the body of male. (Males are very rare in this species.) B) Anterior portion of the body of juvenile. C) Anterior portion of the body of immature female. D) Tail of male. E) Tail of juvenile. F) Immature female. G) Mature female. H,I) Tail of immature female. J) Tail of mature female. (After Dasgupta *et al.*, 1968, modified).

Table 7. Known hosts of *Rotylenchulus macrosoma*.

Common name	Scientific name
Chickpea	<i>Cicer arietinum</i> L.
Corn cv. N-170	<i>Zea mays</i> L.
Olive	<i>Olea europaea</i> L.
Potato	<i>Solanum tuberosum</i> L.
Snap bean cv. Contender	<i>Phaseolus vulgaris</i> L.
Soybean cv. Lee	<i>Glycine max</i> (= <i>hispida</i>) (L.) Merr.
Tomato cv. Hosen	<i>Lycopersicon esculentum</i> Mill.

and Grullon, 1975; Stokes, 1982), but not in South America. In Africa, *R. parvus* occurs in Ivory Coast, Kenya, Malawi, Mauritius, Mozambique, South Africa, Zaire, Zambia, and Zimbabwe (Dasgupta *et al.*, 1968; Germani, 1978a; Van den Oever and Mangane, 1992). In Asia, it has been found only in Haryana state in India (Bajaj and Bhatti, 1987). In Australia, it occurs in Queensland (Colbran, 1964). Known hosts of *R. parvus* are mainly herbaceous plants and a few fruit trees (Chinappen *et al.*, 1988; Dasgupta and Raski, 1968; Heyns, 1976; Van den Oever and Mangane, 1992) (Table 8). Maize is a good host for *R. parvus*. In contrast to results obtained with *R. reniformis*, maize was found in South Africa to be a far better host for *R. parvus* than cowpea, with populations increasing 3000% during a 3-year maize monoculture (Furstenberg and Heyns, 1978). Sugarcane is another good host of *R. parvus* in South Africa (Van den Berg and Spaull, 1981).

Rotylenchulus parvus is a parthenogenetic species (males are extremely rare), but otherwise has a life cycle similar to that of other reniform nematodes. The duration of the life cycle from egg to egg is 26-36 days at 24-28°C (Dasgupta and Raski, 1968). *Rotylenchulus parvus* is listed by the Animal and Plant Health Inspection Service of the United States Department of

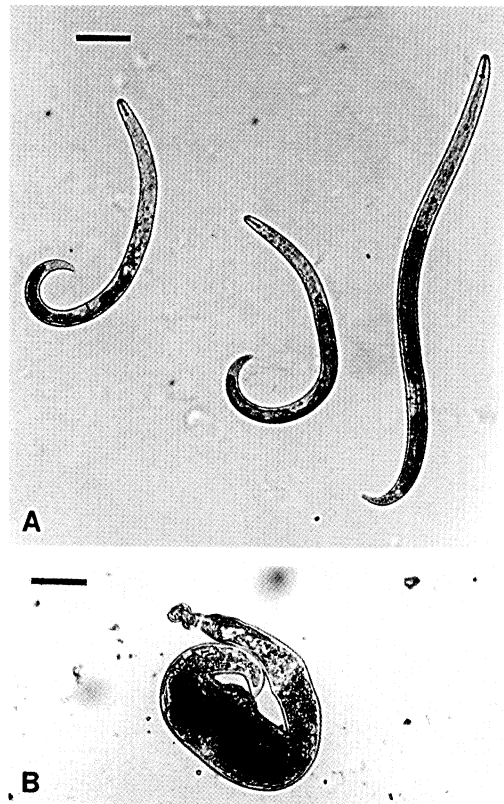


Fig. 19. Selected life stages of *Rotylenchulus parvus*. A) Immature females of *R. parvus* (two on the left) are compared with that of *R. reniformis* (one on the right), which has a longer body. B) Mature female of *R. parvus*. Scale bars = 34 μ m in A and 36 μ m in B. (After Lehman and Inerra, 1990).



Fig. 19. Selected life stages of *Rotylenchulus parvus*. A) Immature females of *R. parvus* (two on the left) are compared with that of *R. reniformis* (one on the right), which has a longer body. B) Mature female of *R. parvus*. Scale bars = 34 μm in A and 36 μm in B. (After Lehman and Inserra, 1990).

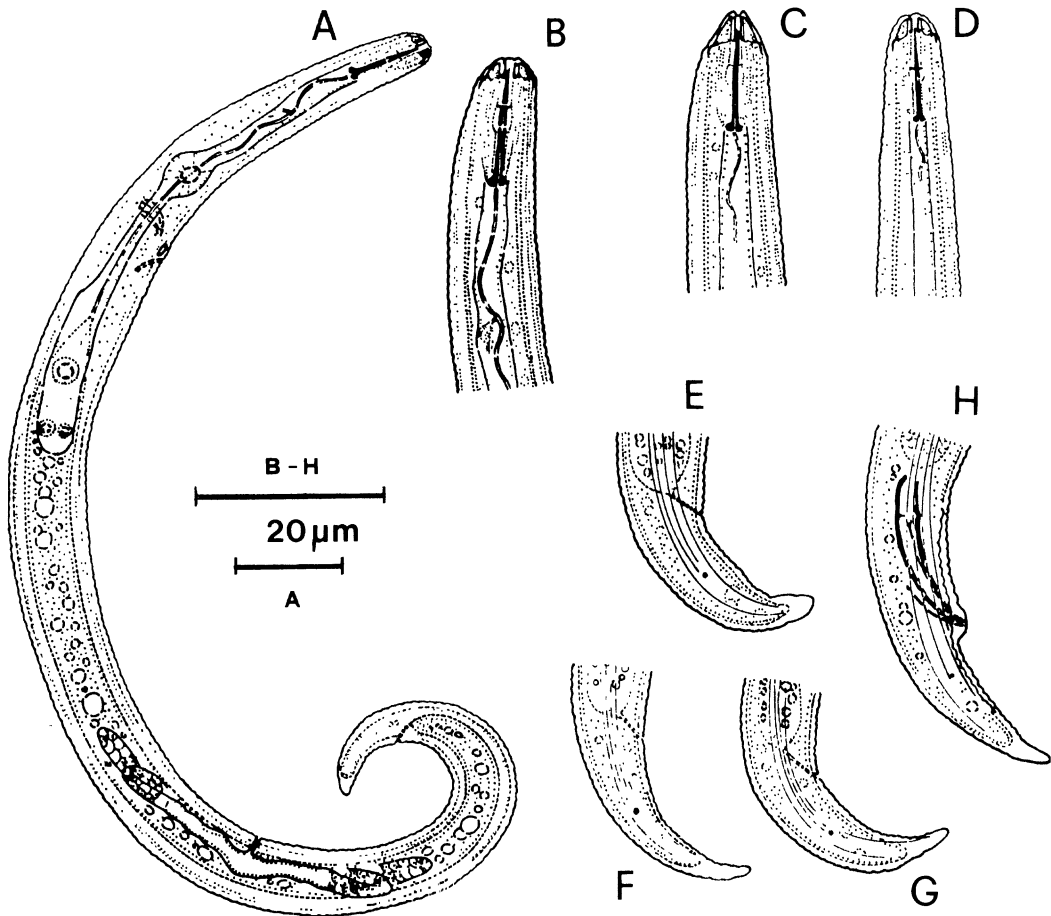


Fig. 20. Known life stages of *Rotylenchulus anamictus*. A) Immature female. B) Anterior portion of the body of immature female. C) Anterior portion of the body of juvenile. D) Anterior portion of the body of male. E) Tail of juvenile. F,G) Tail of immature female. H) Tail of male. (After Dasgupta *et al.*, 1968, modified).

Agriculture as a noxious organism subject to quarantine restriction by Brazil.

ROTYLENCHULUS SPECIES OF MINOR ECONOMIC IMPORTANCE

Rotylenchulus anamictus

This species (Fig. 20) was described from male and immature female specimens collected from the rhizosphere of *Acacia* in Merca, Somalia (Dasgupta *et al.*, 1968). It is similar to *R. parvus* from which

R. anamictus can be separated by the presence of males and a more posterior vulva position in vermiform females ($V = 62-72\%$ vs. $60-66\%$ for *R. parvus*). Swollen females, biology, and hosts of *R. anamictus* are not known.

Rotylenchulus brevitubulus

This species was described from male and immature female specimens collected from an unidentified shrub in the savanna

Table 8. Known hosts of *Rotylenchulus parvus*.

Common name	Scientific name
Barley	<i>Hordeum vulgare</i> L.
Bermuda grass	<i>Cynodon dactylon</i> (L.) Pers.
Corn	<i>Zea mays</i> L.
Upland cotton	<i>Gossypium hirsutum</i> L.
Cowpea	<i>Vigna unguiculata</i> (L.) Walp
Macadamia	<i>Macadamia</i> sp.
Pearl millet	<i>Pennisetum americanum</i> (= <i>glaucum</i>) (L.) K. Schum.
Papaya	<i>Carica papaya</i> L.
Potato	<i>Solanum tuberosum</i> L.
Sugarcane	<i>Saccharum officinarum</i> L.
Sunn hemp	<i>Crotalaria juncea</i> L.
Tobacco	<i>Nicotiana tabacum</i> L.
Thyme	<i>Thymus</i> sp.
Tomato	<i>Lycopersicon esculentum</i> Mill.

of Grunau, in west South Africa/Namibia (Van den Berg and Spaull, 1981) (Fig. 21). It has juveniles with a bifurcate tail tip unlike the undivided tail tip of the juveniles of other reniform nematodes. The distance between dorsal esophageal gland orifice and the stylet base of immature females is $< 10 \mu\text{m}$ ($6.0\text{-}7.5 \mu\text{m}$), whereas it is $> 10 \mu\text{m}$ for immature females of other *Rotylenchulus* species. Swollen females, biology, and hosts of *R. brevitubulus* are unknown.

Rotylenchulus clavicaudatus

This species was described without swollen females from specimens collected from the rhizosphere of *Strelitzia* sp. in Port St. Johns, Transkei, South Africa (Dasgupta *et al.*, 1968) (Fig. 22). Additional specimens and one swollen female were collected several years later from a sugarcane field at Mount Edgecombe, South

Africa (Van den Berg and Spaull, 1981). This species has juvenile and female stages with a distinct clavate tail tip. Males have both clavate and tapered tail tip. Biology and hosts of *R. clavicaudatus* are unknown.

Rotylenchulus leptus

This species (Fig. 23) was described from immature female specimens collected from the rhizosphere of *Bambusa* sp. at Gwela in southern Zimbabwe (Dasgupta *et al.*, 1968). Additional specimens were found in cultivated and uncultivated land in South Africa (Kleynhans *et al.*, 1996). It is apparently parthenogenetic and is very similar to *R. parvus*. It can be separated from *R. parvus* by its longer hyaline portion (h) of the immature female tail ($h = 3\text{-}7 \mu\text{m}$ vs. $< 3 \mu\text{m}$ for *R. parvus*). Swollen females, biology, and hosts of *R. leptus* are not known.

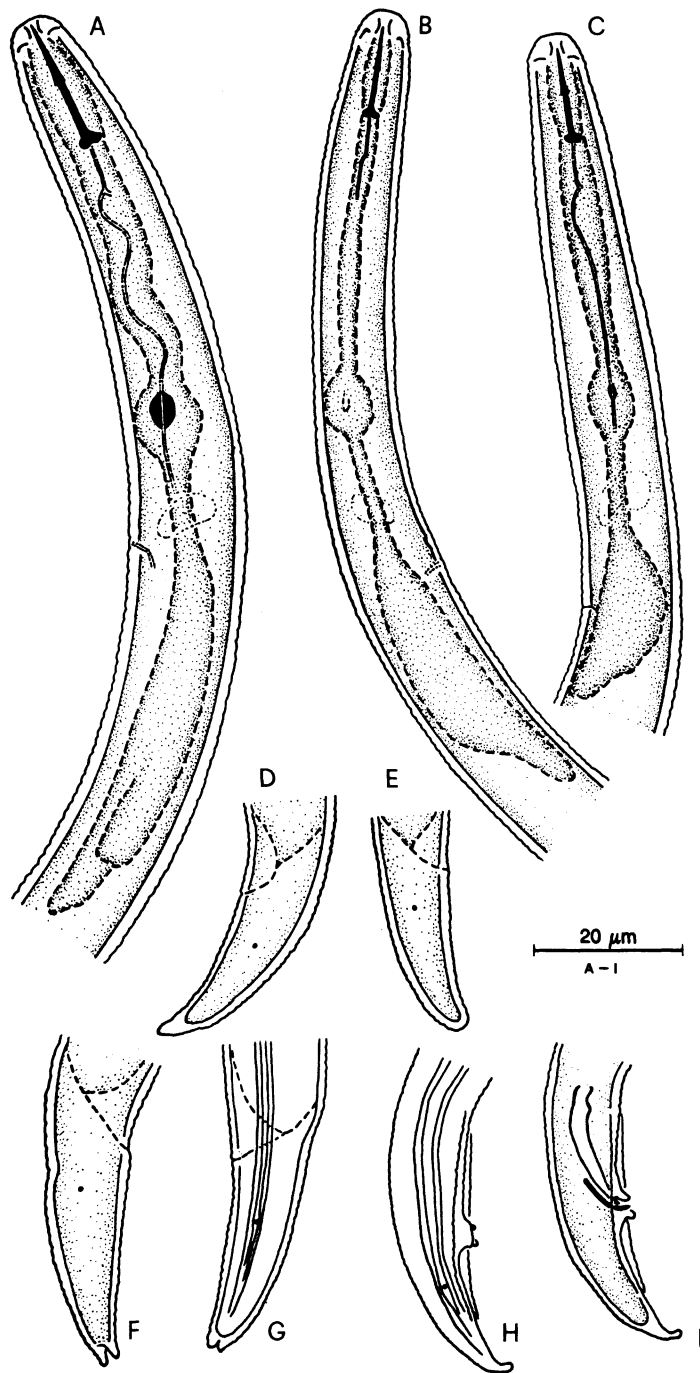


Fig. 21. Known life stages of *Rotylenchulus brevityubulus*. A) Anterior portion of the body of immature female. B) Anterior portion of the body of male. C) Anterior portion of the body of juvenile. D,E) Tail of immature female. F,G) Bifurcate tail of juvenile. H,I) Tail of male. (After Van Den Berg, 1990, modified).

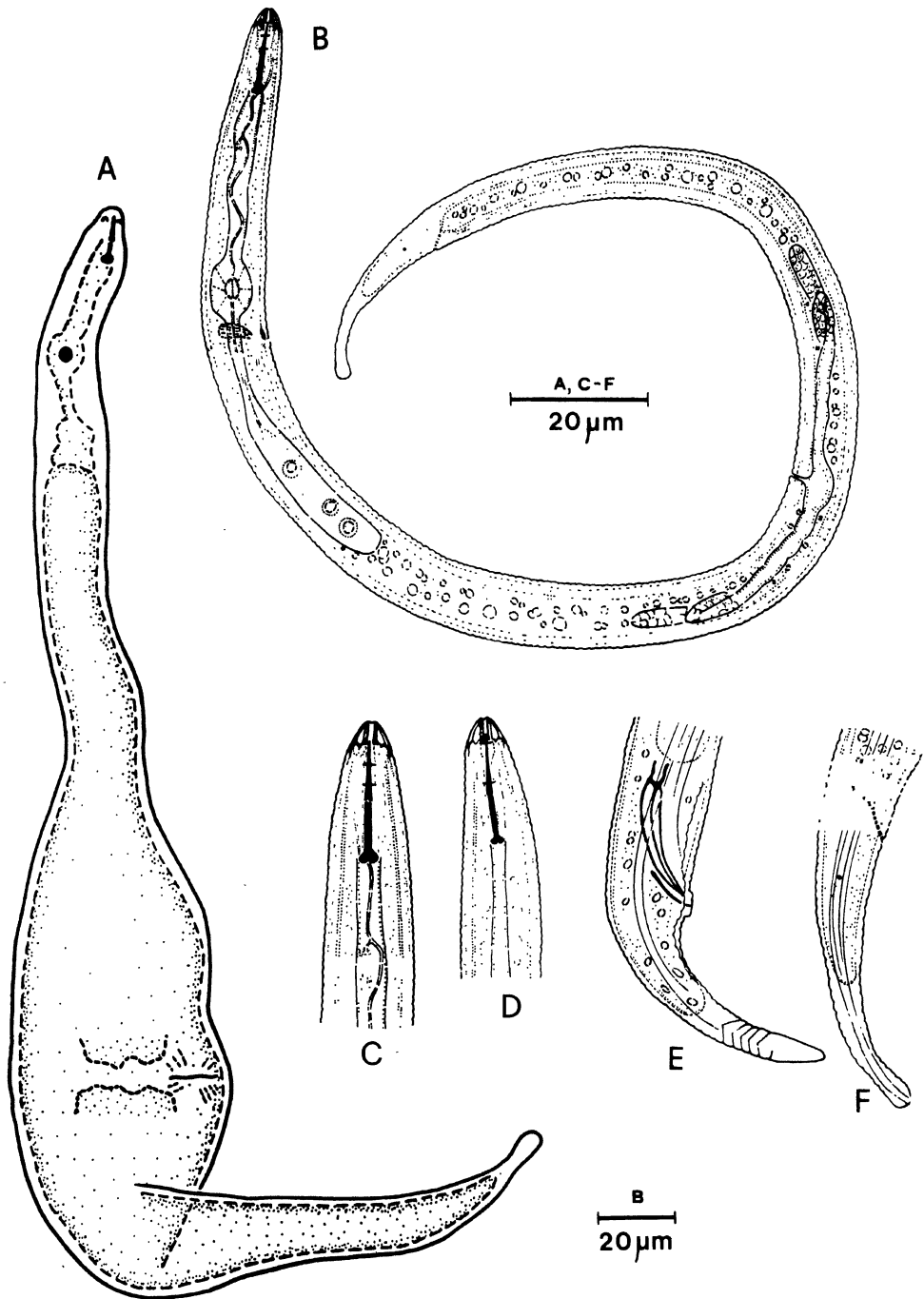


Fig. 22. Life stages of *Rotylenchulus clavicaudatus*. A) Mature female. B) Immature female. C) Anterior portion of the body of immature female. D) Anterior portion of the body of male. E) Tail of male. F) Tail of immature female. (After Dasgupta *et al.*, 1968, and Van Den Berg and Spaull, 1981, modified).

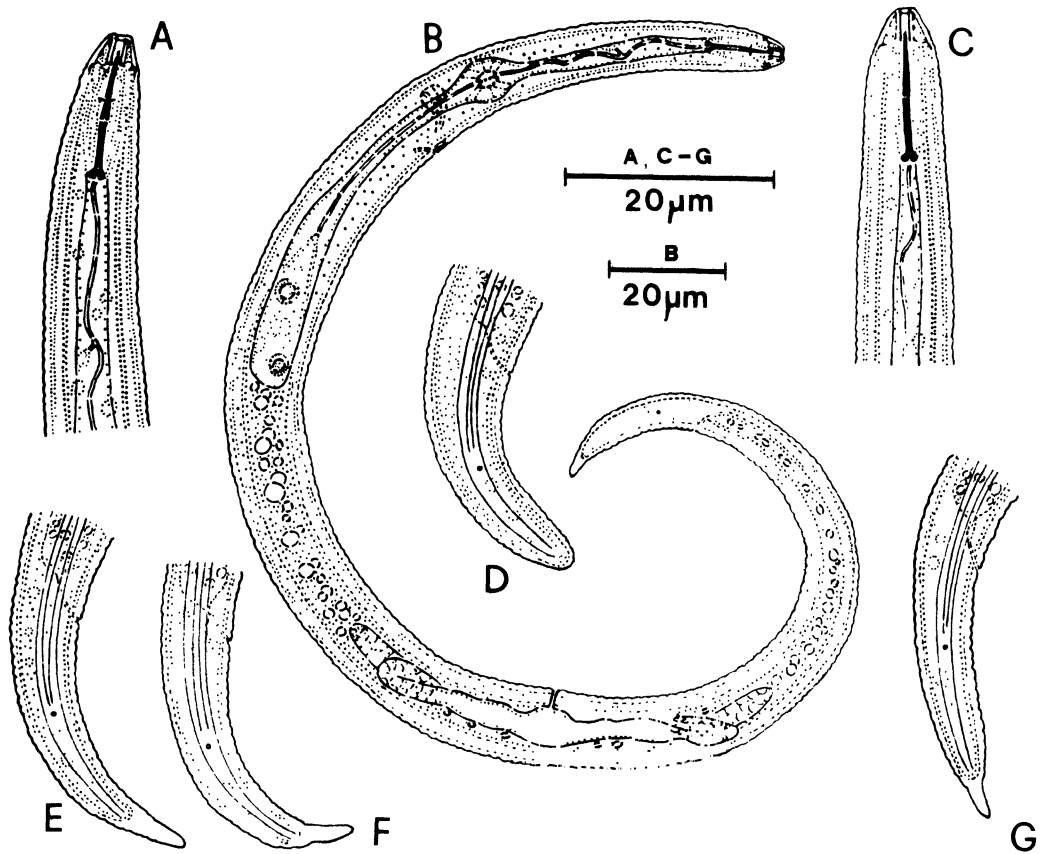


Fig. 23. Known life stages of *Rotylenchulus leptus*. A) Anterior portion of the body of immature female. B) Immature female. C) Anterior portion of the body of juvenile. D) Tail of juvenile. E-G) Tail of immature female. (After Dasgupta *et al.*, 1968, modified).

Rotylenchulus sacchari

This species was described from male and immature female specimens collected from a sugarcane field in Heatonville, Natal, South Africa (Van den Berg and Spaull, 1981) (Fig. 24). The immature females have a longer stylet than those of other reniform nematodes (29.0-32.5 μm vs. < 27 μm for other reniform nematodes) and a bluntly rounded tail terminus. Swollen females, biology, and hosts are not known.

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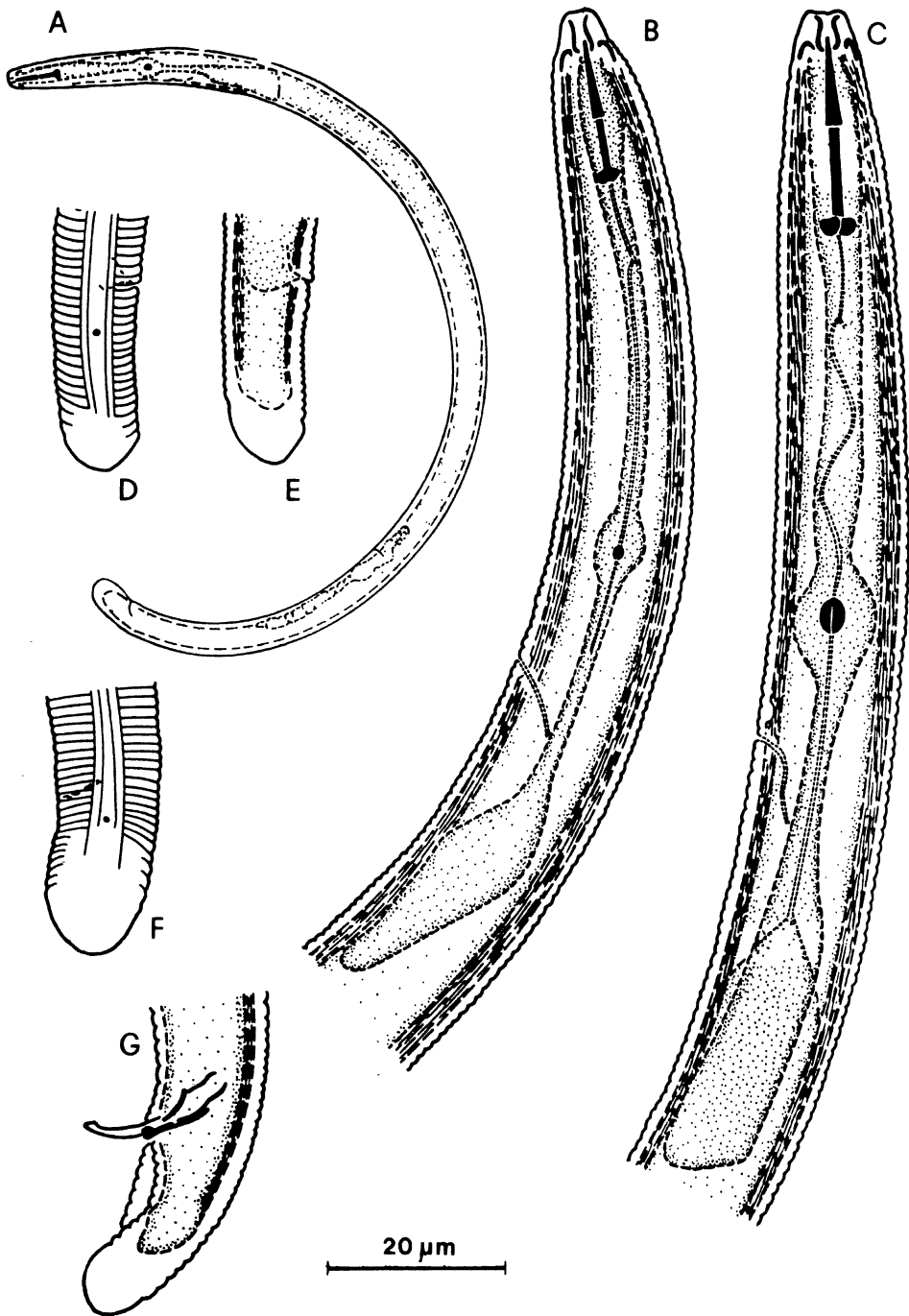


Fig. 24. Known life stages of *Rotylenchulus sacchari*. A) Immature female. B) Anterior portion of the body of male. C) Anterior portion of immature female. D, E) Tail of juvenile. F) Tail of immature female. G) Tail of male. (After Van den Berg and Spaull, 1981, modified).

ical Society of Washington, publisher of the Proceedings of the Helminthological Society of Washington; the Plant Protection Research Institute of Pretoria, South Africa, publisher of Phytophylactica; Society of Nematologists, publisher of the Journal of Nematology; and the Soil and Crop Science Society of Florida, publisher of Soil and Crop Science Society of Florida Proceedings.

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